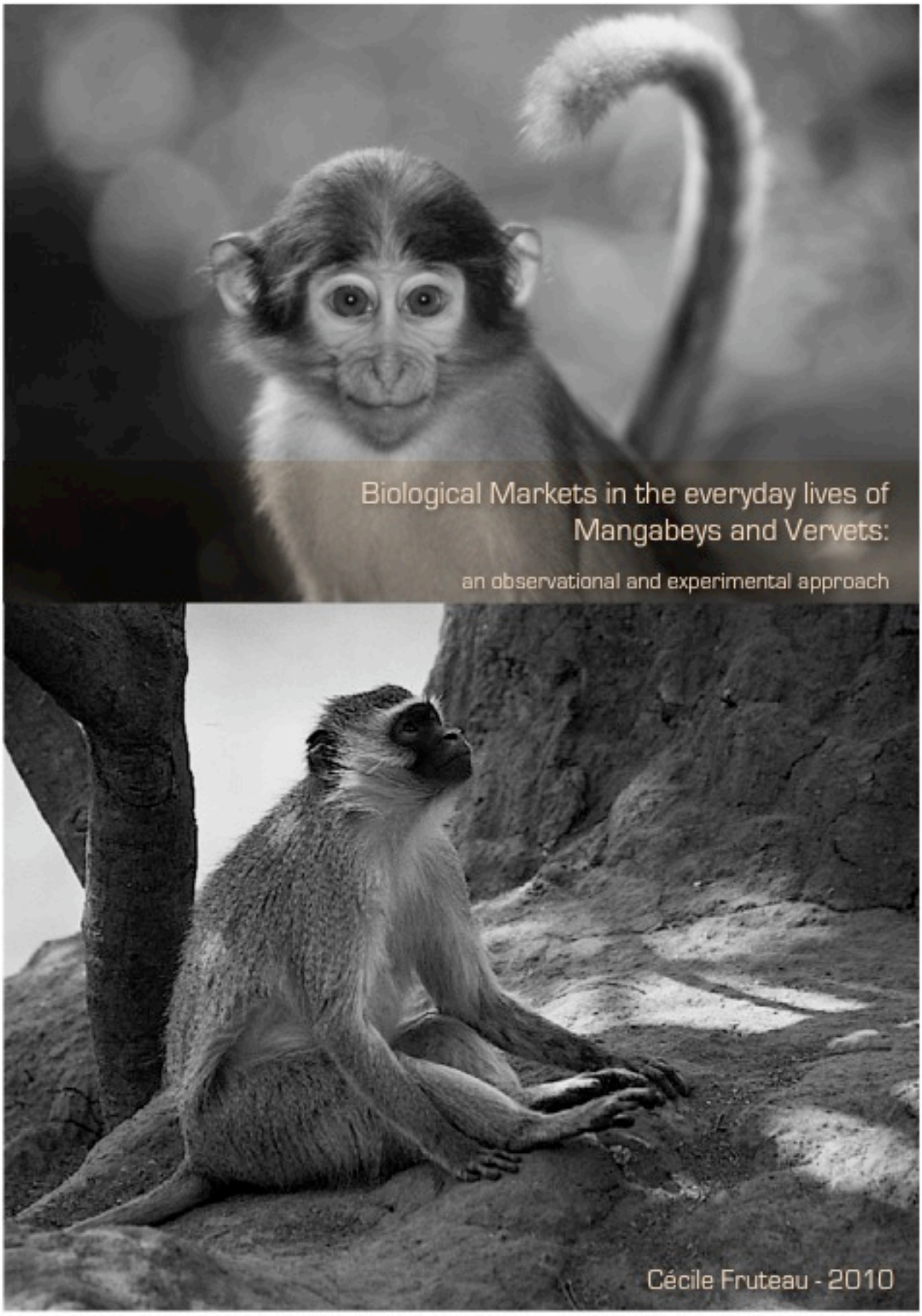

Biological Markets in the everyday lives of
Mangabeys and Vervets:
an observational and experimental approach
Cécile Fruteau - 2010

Biological markets in the everyday lives of mangabeys and vervets: an observational and experimental study

"Proefschrift ter verkrijging van de graad van doctor aan de Universiteit van Tilburg, op gezag van de rector magnificus, prof. Philip Eijlander, in het openbaar te verdedigen ten overstaan van een door het college voor promoties aangewezen commissie in de aula van de Universiteit op Dinsdag 21 December 2010 om 14.15 uur door Cécile Fruteau geboren op 11 Februari 1977 te Arcachon, Frankrijk".

Supervisors:

Prof. Dr. Eric van Damme

Prof. Dr. Ronald Noë

Committee:

Dr. Lisbeth Sterck

Prof. Dr. Jan A.R.A.M. van Hoof

Prof. Dr. Redouan Bshary

Prof. Dr. J.J. Potters

Prof. Dr. Charles N. Noussair

NWO (**Evolution and Behaviour 051-12-036**) provided financial support for this study.

To my family, who supported me during all the steps of this long journey. With love…

CF

To the question many people asked me during all those years (especially those who were astonished by the fact that an institution could actually pay for my work…), here is a nice answer:

" What is all that for?"

« On the most basic level, what we are trying to do in science is to understand our world. Predictions are an excellent means of testing our comprehension, and once we have the comprehension, applications are inevitable; but the basic aim of scientific activity remains the comprehension itself. »

From Robert Aumann – *What is game theory trying to accomplish?*

Table of Contents

SUMMARY

Cooperation between unrelated partners has long been an evolutionary paradox: why would organisms sustain severe costs in order to increase the fitness of a prefect stranger? Many models tried to tackle the issue. Some focused on the fact that cooperation would not evolve if partners do not control each other (reciprocal altruism model by Trivers, parcelling model by Connor, and so forth). Other models switched the emphasis from partner control to partner choice as an effective tool to enforce cooperation. It is the case of the biological market theory (BMT) developed by Noë & Hammerstein, in which cooperative interactions between organisms are similar to market exchanges. Individuals compete to get the best bargain possible and switch partners if the interaction does not yield sufficient benefits. In this project we extensively tested the predictions derived from BMT and showed how they provide insights into the social interactions in two different primate species. We worked with one group of sooty mangabeys (*Cercocebys atys*) from the Taï National Park in Ivory Coast and two groups of vervet monkeys (*Chlorocebus aethiops*) from the Loskop Dam Reserve in South Africa. We first investigated naturally occurring exchanges: grooming-grooming, grooming-infants and grooming-sex exchanges. For each set of exchanges, we tested predictions derived from the law of supply and demand and predicted that grooming investments would follow the fluctuating availabilities of the sought commodities. We also investigated how outbidding competition and effects such as sexual receptivity or infants maturity could affect the value of the commodity. We demonstrated that individuals tended to choose partners who had little leverage on them and they differentiated between partners they often interacted with and the rest of the group. They also invested large amount of grooming to obtain rare commodities. We secondly investigated grooming exchanges in an artificial setup. The field experiments demonstrated that monkeys quickly understood new market situations and easily adapted to it. They did so by modifying grooming ratios in very few trials and also by reducing their aggressive behaviours. We showed that their self-control was acquired through a queuing-to-learn system and that it seemed to be socially enhanced.

AKNOWLEDGEMENTS

I would like to thank both Eric and Ronald for having given me the opportunity to perform this project. I think both of them will be relieved now that it is the end. I would not of course fathom why… I was such a great sport! But well, the fieldwork was quite challenging, the writing of the papers too. Unfortunately nowadays, working with social monkeys seems to lead to endless troubles in terms of dependency of the data or pseudoreplication (!). Nicolas Poulin (who I greatly thank here as well), our biostatistician, would certainly know since I ran in his office each time I had a problem (and still do!).

I would like to thank all the people in the field. They certainly made it possible and a lot easier: Erica and Jen: the soul sisters, the first, a friend with the joyful iron spirit, the second, a friend with the wise iron spirit; Alex and Eléonore: the dream team of the darkest times; Valérie, Stéphane and Sylvain: the amazing and unexpected helpmates; Albert, Dale, Big D, Alan and the people from the reserve.

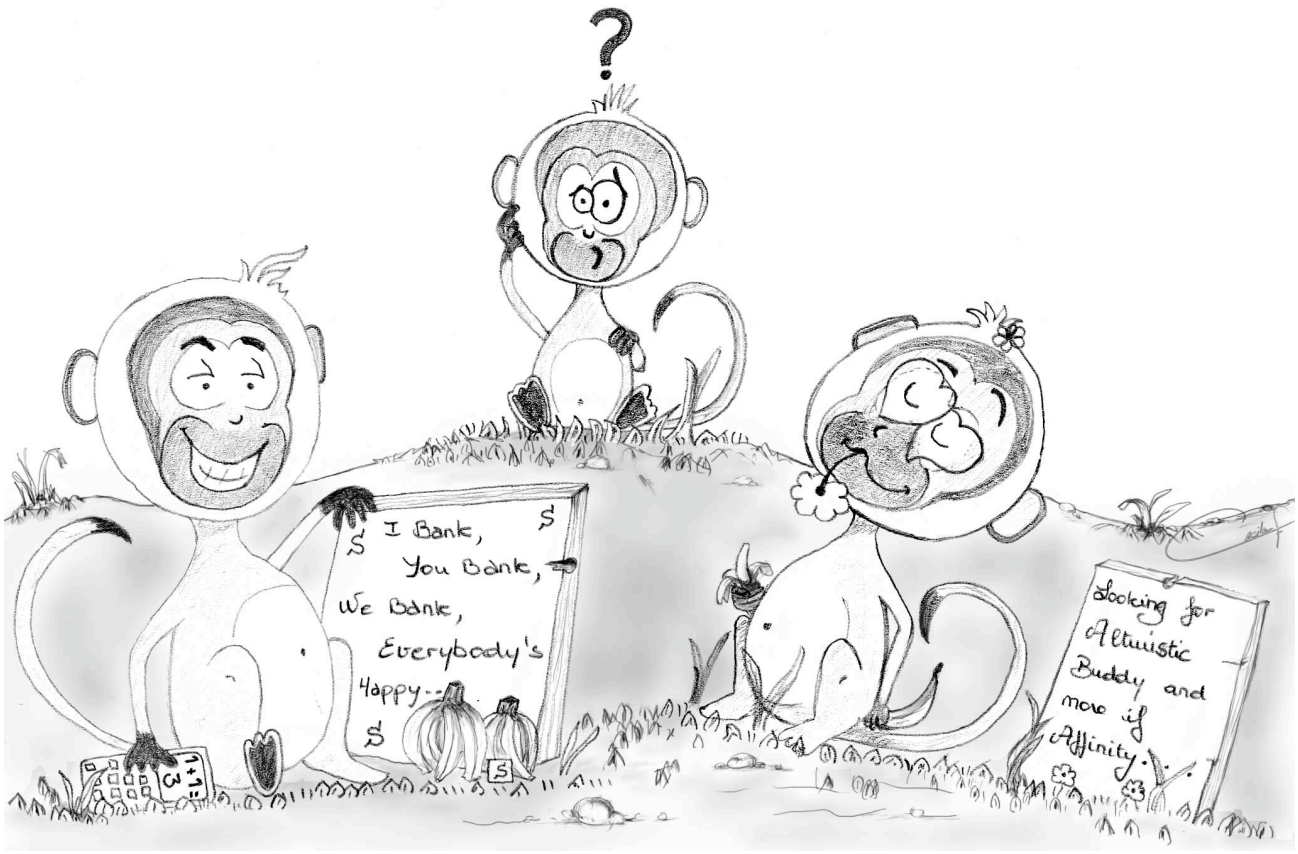
I would also like to thank all the people who remained in Europe and made it a nicer place: all the team from Strasbourg: Odile (no comments!), Cédric, the three Marie (s), Bernhard and Claudia, Valérie (again!), Armand, Coin Coin, Riccardo, AnneCo, Clémence and Coralie. In the Netherlands: Daniël, the guys from De Bilt and many members of the staff from the University.

Finally I would like to thank my family: my mum, always there, the one I'd like to become eventually; my two brothers: two brilliant minds no less; Xi: the little mouse from China; my grand-parents and godmother: the stable place of love; my father: now a free spirit (just hope you can see me from where you are) and of course my two big loves: Jmi: here again, no comments… (except when you just drive me crazy when you try to manage everything) and Lou: just as a future reminder: you can't walk yet but you speak English (haha!!).

CHAPTER 1

EXPLORING THE PATHS BETWEEN COMPETITION AND COOPERATION BETWEEN UNRELATED PARTNERS

A general introduction to biological market theory



C & JM Fruteau

INTRODUCTION

Since Darwin's natural selection theory, evolution, or the structural and behavioural changes observed throughout generations, was assumed to be based on competition and the survival of the fittest. The subsequent arising conflicts explained most traits, ranging from diets variations to the development of secondary sexual characters. Competition was, in turn, assumed to be based on adaptations the modalities of which constitute one of the main purposes of modern studies in biology. All living individuals show adaptations to their environment: most of their actual genetic and behavioural traits were kept and transmitted throughout generations since they usually enhanced their owner's survival in response to new or modified surroundings. A textbook example, now controversial, was the case of the birch moths in Great Britain (Kettlewell's work reviewed in Ridley 2004, and see Brakefield 1987). The moths usually rest on the white birch bark during the day and are less conspicuous when they are brightly coloured with small black dots. Prior to the industrial period, this clear phenotype constituted about 98% of the population. However, when increasing pollution made their resting substrates darker, blacker moths became less susceptible to predation and had greater chances to survive and reproduce. Therefore, the dark trait was passed on and in polluted areas the dark phenotype is now the most represented. Experiments also showed that moths carefully chose the substrate on which they would rest, clear moths selecting clear barks and dark moths resting on dark ones. Obviously moths' survival is defined by both their colour and their behaviour.

Behaviours can either be adapted, i.e. they are genetically coded, selected and expressed, or result from individual plasticity, i.e. they are expressed through learning, temporary physiological adjustments or maturation. On the ultimate level, behaviours are selected in the sense that they benefit their owner's fitness. In behavioural ecology, the fitness of an individual "having an array x of phenotypes", is described as "the probability s(x) that the individual will be included among the group selected as parents of the next generation" (definition from Wikipedia).

It is important to understand how behaviours can enhance individuals' survival and reproductive efforts on a proximal or mechanistic level. It is also important to understand how they evolved from a completely different historical function to become what they are nowadays. For example, the human smile as well as the mandrill grin are a bizarre exception in primates. Indeed, most non-human primates would see this bared teeth display as an expression of either fear or submission (but see Petit & Thierry 1992 for an example of affiliative function). Both the smile and the grin are thought to have derived from their submissive original function to act as an appeasing behaviour enhancing one-shot cooperation among strangers (see for example Scharlemann *et al*. 2001, Schmidt & Cohn 2001, Balliet 2010).

In this context in which competition seems to drive organisms' structural and behavioural changes, the emergence and maintenance of cooperative behaviour may prove difficult to explain. Indeed for many authors (e.g. Trivers 1971, De Waal 2000) cooperation would be described as a succession of exchanges in which individuals take turns in receiving beneficial services (and/or commodities) but also in losing some fitness (except if they succeed in taking turns) for the benefit of another individual. The costly actions would then be called altruistic episodes. The losses would theoretically be more easily explained when cooperation takes place among related partners. Hamilton (Kin Selection Theory 1964, see Clutton-Brock 2002 for a review) demonstrated that the degree of genetic relatedness influenced cooperative interactions between closely related individuals. His theory also allowed making predictions on how selection operates in this case: the genetic information coding for 'altruistic behaviour' can be selected for if this altruistic behavior is directed at individuals that carry the same genetic information with a high probability (which is the case for close relatives of the altruist). However, cooperation and its associated losses are more difficult to explain when they occur between unrelated partners. As Noë (2006) writes: "the art of cooperation consists of investing the right amount in the right partner at the right moment". When individuals choose the wrong partner, they can sustain severe losses. When they invest in the relation and bet on the hypothetical beneficial returns, they may

never receive them. Why would they take such risks when partners are not even affiliated? How could selection possibly favour cooperation among unrelated partners?

Cooperation among unrelated individuals

Trivers' idea to tackle cooperation occurring between unrelated partners is quite simple: it may be beneficial to help another if one can expect to be helped in return in the future. In his Reciprocal Altruism Theory (1971), the cost of helping would be compensated by the expected return benefit and the behaviour would evolve by natural selection. He designed a model in which a population of N individuals is composed of cooperative members displaying genetically coded altruistic behaviours (a_2a_2 genotype) and of egoist members presenting the alternative unaltruistic allele (a_1a_1 genotype). He also implemented the notion that altruistic reciprocation is enhanced by the exchange itself and not by the fact that one allele directly benefits its equivalent duplicate in another individual: the reciprocation can take place between conspecifics as well as individuals belonging to different species. He found that reciprocal altruism is more likely to appear in species with 1- an extended life span and a high degree of mutual dependence that can provide many altruistic situations, 2- a low dispersal rate and 3- an egalitarian hierarchical system allowing more symmetrical relations. Furthermore, the best answer to non-reciprocation is to curtail any further altruistic interaction with this partner (i.e. 'defect'). Based on the dyadic relationships between individuals that are repeatedly and symmetrically interacting with each other, reciprocal altruism is often compared to the Tit-for-Tat strategy emerging from the iterated Prisoner's Dilemma game (Trivers 1971, Axelrod & Hamilton 1981, Box 1).

Currently viewed as one of the many mechanisms that could enhance the emergence of cooperation between unrelated partners (Sachs et al. 2004, Lehmann & Keller 2006, West et al. 2007 a), reciprocal altruism is unlikely to occur in species other than humans (West et al. 2007) because the conditions that are required are extremely restrictive (e.g. Hammerstein 2003, Stevens et al. 2005 a). Reciprocal altruism theory inspired a large body of theoretical and empirical work

on cooperation among unrelated partners, however. Many authors (see Sachs et al. 2004 for a review) have attempted to design models that could explain various examples of cooperative behaviours.

Box 1. Supergames and Prisoner's Dilemma rules.

Supergames are characterised by a series of interactions of the same game played between the same partners who can pick from the same set of strategies. The latter is not necessary. After each interaction, the game is repeated with a certain probability. When it is difficult to obtain a stable cooperation in just one round and when the number of rounds is large enough, complex strategies can arise as solutions for the supergame. A usual game chosen for predicting cooperation and altruism is the Prisoner's Dilemma game. Its rules are quite simple: two players, playing simultaneously and without knowing what the other chose to do, can either cooperate C or defect D. The payoffs are such that if the players are rational, each should think that whatever the choice of the other is, he/she should defect:

Table 1. Prisoner's Dilemma payoffs.

		Player B	
		D	C
Player A	D	P, P	T, D
	C	D, T	R, R

For this game to be a dilemma, the payoff for the Temptation T (I defect, the other cooperates) should be higher than for the Reward for mutual cooperation R (we both cooperate), that should also be higher than the Punishment P (we both defect), that should in turn be higher than the Defection D (I cooperate, the other defects):
$T > R > P > D$

In single round games and independently from any partner's playing decision, the rational option to get a payoff is defection. In iterated versions however, evolutionary stable cooperation can emerge from various strategies such as "Tit-for-Tat" (the first player cooperates on its first move and then reproduces whatever its partner is playing; see Dugatkin 1997 for a review on ESS). When such an evolutionary stable cooperation arises, defecting players cannot invade the population anymore, which makes the game robust to defection.

For instance, Dugatkin and Wilson (1991) as well as Enquist and Leimar (1993) tried to tackle the mobility issue and presented models in which the change of partner was made possible. They found that mobility seriously affects the evolution of cooperation as a single mobile free riding cheater can easily exploit a population of cooperators. Most other models focussed on how players could exert control over their partners through immediate sanctions in case of defection.

For example Connor developed the parcelling model (1995) in which defection is not a advantageous option. Dyads of individuals, still caught in an iterated prisoner's dilemma, reduce the risk of exploitation by delivering their goods and services in small packages. The goods parcelling ensure that partners benefit more from reciprocation than from defecting and look for another partner. Hence parcelling changes the payoff matrix of each round of the game in such a way that it is no longer a prisoner's dilemma. The model seemed to work well for egg trading in simultaneous hermaphrodites fish (Connor 1992) and for allogrooming in impalas (Connor 1995) but only when the animals are not in a two-player game. When it is the case, they cannot switch partners and parcelling make no sense (see also Friedman & Hammerstein 1991). The major technical problem of parcelling model however resides in the difficulty for predicting the proportion of parcelling that would fulfil the requirements of the payoff matrix. Roberts and Sherratt (1998) developed the idea of the parcelling model further and proposed the "raising-the-stakes" (RTS) model in which animals can arrive at taking greater risk of exploitation by first building trust with their partners. This strategy can by definition only be applied by individuals that never met their partner before. They would start with delivering small packages, and then increase the costs of the portion delivered in each round, as long as the partner matches the investment (see Milinski 1987 for an example of Tit-for-Tat allowing cooperation in fish, but see Noë 2006 for a critique).

Some other models (e.g. Batali & Kitcher 1995, Bull & Rice 1991, Noë 1990, Noë et al. 1991, Noë & Hammerstein 1994) switched from the dyadic, 'partner control' aspect of cooperation to the dynamics of cooperation in which partners have the option to choose and switch partner (see Bshary & Noë 2003). Such 'partner choice' models emphasize the fact that most individuals would risk some investments to initiate interactions because these costs are reduced if cooperation with a partner is better than defecting and not cooperate at all. Furthermore, individuals can terminate cooperative interactions whenever the selected partner does not produce the expected benefits. Hence, these models contemplate the fear of partner

switching as a potent component for partner control and they consider partner choice as a likely mechanism for the evolution of cooperation. The emphasis is not on keeping track of past interactions but is rather on choosing the best partner possible at a precise moment.

Cooperation and markets

In the rest of this manuscript I use the following definition to describe cooperation: "all interactions or series of interactions that, as a rule (or 'on average'), result in net gain for all participants" (Noë 2006). The overall net gain can be immediate or reached over long-term periods. In this context, I view cooperative behaviour as an investment with a risk of no or insufficient returns.

Studies based on sexual selection theory reveal that animal reproductive strategies are characterized by asymmetric relationships between genders essentially due to different reproductive potentials (see Andersson 1994 for a review). The operational sex ratio (OSR; Emlen, and Oring 1977) is almost always skewed in favor of the females. This implies that male reproductive success is likely to be limited by the access to receptive females and that there will be competition among males over access to such females. Males are often seen to display structural traits and/or behaviours that potentially affect their survival and are not directly linked to their reproductive apparatus (sexual secondary characters). It is for example the well-known case of the peacock tail that conveys huge energetic and survival costs for males. According to Zahavi and Zahavi's handicap principle (Zahavi 1975, Zahavi & Zahavi 1997), these handicaps constitute an honest signal for females to evaluate males' abilities to survive and to choose among many potential partners.

The analogy between animal reproductive strategies and human trading systems led to the oldest market paradigm in biology: the mating market. Probably because of the extreme attention given to partner control in reciprocal altruism, the importance of partner choice as well as

outbidding competition outside the mating market has long been put aside. Yet, many exchanges are observed within and between species and seem to fit the economic law of supply and demand. It is almost impossible to predict the exact exchange rates when the supply and demand ratios vary. However, it is often possible to predict in which direction the exchange rate will move: the fewer commodities are available, the higher are the respective offers. For example, pied kingfisher breeders and their related helpers accept unrelated helpers more readily if these potential mate competitors provide enough food to alleviate the costs for accepting them in the group. The amount of food brought to the nest by each of the secondary helpers increases with the number of secondary helpers attending the nest (Reyer 1986). Similarly, the quantity of nectar provided by lycaenid butterfly larvae varies according to the species and the number of ants that can protect them (Leimar & Axén 1993, Axén 2000, Pierce et al. 2002). It is sometimes tricky to assess the real amount or availability of a commodity. It is the case for example in exchanges occurring in mycorrhiza and rhizobia associations. West and collaborators (2002) showed that the exchanges were altered by the presence of abiotic resources brought via fertilizers. Hence, the difficulty in studying predictions derived from the law of supply and demand is to properly define the actors of each trader class and estimate the amount of commodity they really hold. When such estimations are erroneous, results can wrongly assumed that an exchange does not follow market rules (see Colmenares et al. 2002, Schino et al. 2003, Gumert 2007b for further discussion).

Confronted with the evidence that many biological systems were characterised by two distinct classes of traders controlling different commodities and that partner choice influenced many animals' traits of life, Noë and Hammerstein (1994, 1995, see also Chiang 2010) proposed that basic human market theory becomes a general framework for explaining cooperation. Biological markets is formalised as follows (adapted from Noë 2001):

1- Each class is composed with either conspecifics or individuals belonging to different species but offering the same commodity, the value of which leads to outbidding or contest competition among its members.

2- Behavioural mechanisms such as partner choice, competition or audience effects determine how the association between trading pairs is settled.

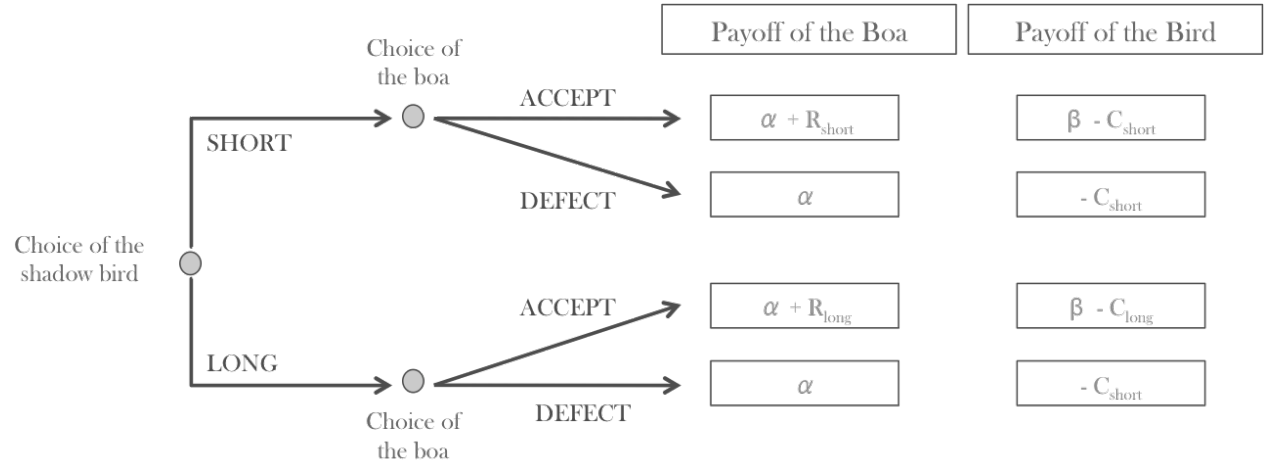
The model predicts that 1- partner choice depends on expectations of better profits one can get with a partner rather than with another, that 2 - members of the more common trading class compete over access to the rare partners, that 3 - competition increases the value of the exchanged commodity, that 4- the supply and demand market law determines the flexible values of exchanged commodities: when a commodity is scarce, it is pricy and that 4- commodities can be advertised.

In biological markets, Noë and Hammerstein (1994) abandoned the dyadic structure that was often used to characterize cooperative interactions. By means of the fictive tale of the "boa constructor" and the "shadow birds" (see the payoffs matrixes in Box 2), they summarized how the number of players could affect the outcome resulting from evolution:

In an open desert area, a female boa constructs a nest mound in which she lays her eggs. Although she can protect them from predation, she can do nothing against solar radiations. She therefore needs to cooperate with a shadow bird female that can provide shade to the eggs thanks to her fan-like tail. In turn, the shadow bird benefits from the cooperation as she can lay her own eggs in the nest and have them protected from predation. Without this active protection from the snake, the bird cannot reproduce. It is assumed that the bird benefits the boa better at shading the eggs than at providing a meal. The amount of shade the bird can provide is morphologically selected and the size of the tail - either short or long – cannot change throughout the nesting period. The snake always benefits from the cooperation but her fitness is positively correlated with the tail length, as more eggs can be shaded. The bird invests in the size of her tail prior to the beginning of the nesting period and a short tail is enough to shade her own eggs. The tail length is negatively correlated with the energy she can allocate to her eggs production.

Box 2. Payoff matrixes with two and three players (adapted from Noë & Hammerstein 1994).

Extensive form of the game with two players:



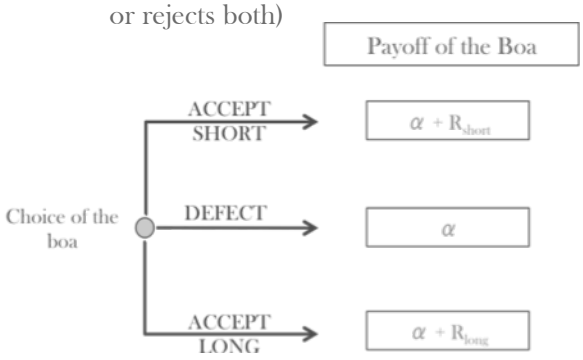
Payoffs of the game with three players (in two steps):

1st step: game among shadow birds
("if the boa is choosy")

Bird 2

Bird 1		Short	Long
	Short	(1/2) β - C_{short}	- C_{short}
	Long	B - C_{long}	(1/2) β - C_{long}

2nd step: boa's choice
(he either chooses one bird
or rejects both)



where α is the boa's basic payoff without cooperation, R is the reward for accepting a bird, C is the bird's cost for her tail and β is the reward the bird gains if she is allowed to cooperate (otherwise her basic payoff is zero).

In the case of a two-player game in which only one boa and one bird are interacting, the bird is scarce since she is the only candidate for shading the snake's nest. Furthermore, her choice prevails on the boa's preferences as she invests in her tail length prior to the nesting period. The ultimate game predicts that the boa will have to cope with what is available and the bird will invest in a short tail. However, in the case of a three-player game in which only one boa but two shadow birds are playing, the previous predictions can be seriously altered. With two candidates,

the boa can exert choice and will prefer the bird with the longer tail. She therefore creates a pressure for the selection of longer tails and birds need to outbid each other in order to be invited to cooperate with the snake. The prediction is then in favor of the birds investing in long tails (under the assumption that growing such a long tail is not too costly).

Box 3. Obligate pollination mutualisms.

The "yucca - yucca moth" association (Pellmyr & Huth 1994, Pellmyr et al. 1996, Pellmyr 1997, Pellmyr & Leebens-Mack 1999):

Moth females oviposit their eggs in the yucca ovaries and actively deposit some pollen on the stigmas to ensure that the lack of pollen will not limit the number of developing seeds, their progenies' food.

To control both moths' over-exploitation and lack of pollinating investment, yuccas use a mechanism of selected abortion of the overloaded fruits as well as the least loaded fruits on which not enough pollen had been brought. The abortion did not evolve under selection by yucca moth. It is a very general mechanism plants use to get rid of unproductive tissue. At best it has been fine-tuned under selection by the moths.

The "senita cactus - senita moth" system (Fleming & Holland 1998):

Even in the presence of other potential pollinators, the evolution of the obligate mutualism was made possible thanks to a greater temporal reliability between the nocturnal opening of the senita flowers and the breeding system of the senita moths.

Photo credits: tamuk.edu, rice.edu & cals.ncsu.edu

This theoretical example introduced the concept of market selection by which traits are enhanced by the formation of mutually beneficial associations. Empirical examples proved that such market selection exists in nature (e.g. birds: Greene et al. 2000; plant/insect associations: Box 3) and I did not focus on that point in the following study. However, it also introduced the

effects of the law of supply and demand with more than two players and the effects of outbidding[1] competition among players of the same trader class, aspects I extensively investigate in the following chapters.

The aims, subjects and outlines of this project

The purpose of this study is to show how the theory of biological markets provides insights into the social interactions in two different primate species. I was particularly interested in grooming exchanges as they held many advantages: 1- In the two studied species they occur on a very regular basis between all members of the group. 2- Grooming interactions are easily recognisable and cannot be mistaken for something else by any observer. 3- Grooming can be easily and objectively measured in terms of time units. However, grooming investments in terms of length cannot directly be translated into values and supply and demand ratios. To estimate the values, it is important to compare grooming investments in various setups. To estimate the supply and demand ratios, it is necessary to add up all the grooming bouts delivered by all group members over a certain period. In the following manuscript I define a grooming session as a series of bouts in which each partner of the grooming dyad take turns. The session ends when there is an interruption of grooming superior to 20 seconds or if the partners move apart.

In most of the following chapters I test predictions derived from biological market theory and mostly find evidence that they can explain exchanges in both species. More particularly, I test predictions derived from the law of supply and demand in different market contexts. I study these markets separately in order to more easily assess the proper trader classes and commodities. I expect that rare commodities hold more value than common commodities. To access such commodities, I expect that individuals would increase their grooming investment in terms of length. Following previous studies (e.g. Barret et al. 1999, Bshary et al. 2008) I also study the

[1] This term of outbidding competition is to contrast with the agonistic competition of Darwin's sexual selection theory.

effects of outbidding competition and power asymmetries between partners. I expect competition to remain at the core of cooperation itself, and subsequently, the identification of any power asymmetries (valuable knowledge, status in the group, etc.) between partners should allow to predict the way payoffs are distributed or fluctuate among partners. I study naturally occurring interactions that would take place daily, during ordinary as well as socially stressful periods such as the mating and birth seasons. I also specifically test the law of supply and demand by performing field experiments.

I worked with two different primate species (Box 4). The sooty mangabeys (*Cercocebus atys*) were observed in the Taï National Park in Ivory Coast. The group was rather large with about 130 members in which I mainly recorded the daily activities of the 35 adult females. Mostly terrestrial, mangabeys can spread over hundreds of square meters while foraging and very low-ranking females have little interactions with the higher-ranking females. During the mating season, many non-resident adult males entered the group for various periods of time. The vervet monkeys (*Chlorocebus aethiops*) were observed in the Loskop Dam Nature Reserve in South Africa. The two groups were rather small compared to the size of the mangabey group, with no more than 15 members, seven adult females in the Donga Group and only four in the Picnic Group. Due to the small size of the groups, most adult females were seen to regularly interact with each other throughout the day. During the study period, no new male entered the groups.

Box 4. Studied species.

Sooty mangabeys (*Cercocebus atys*)

Vervet monkeys (*Chlorocebus aethiops*)

Photo credits: F. Range & S. Aubel

In the first study (Chapter 2) I investigate how adult females distribute reciprocal grooming bouts during periods (1) in which we did not perform any experiments and (2) the females did not go through stressful periods of the reproductive cycle (sexual receptivity; carrying and suckling infants of less than three months). Reciprocal grooming sessions have been thought to reinforce the social bonds between females (Seyfarth & Cheney 1984, Hemelrijk 1994) and usually constitute the major part of their social activity budget. Practically, even if grooming bouts are rather short in time and probably low-cost (Silk 2003), they help reducing fur ectoparasite loads on body parts that one cannot reach by the groomee (Mooring et al. 1996, Zamma 2002) and they enhance the production of beta-endorphins (Keverne et al. 1989) known to cause 'pleasant' feelings. Therefore, they have also been described by Barrett and Henzi (2001) as useful trading means in biological market contexts.

In a first step, I investigate how females of both species are exchanging grooming bouts. I look at the identity of each partner of the grooming dyad to determine whether hierarchy influences grooming investments and whether females privilege particular partners. I expect females to maximise their benefits. They can do so by time matching their grooming investments and choosing to mainly interact with closely ranked partners as a difference of social status should bias the investment towards the lowest-ranking partner of each dyad. Indeed, higher-ranking females may have more to offer (support during conflicts, tolerance at food sites) than just grooming and this leverage should advantage them in the grooming exchange. In a second step, I focus on the reciprocated bouts only. I investigate the way they are distributed within a grooming session. I check for partner control via parcelling (Connor 1995) and trust building (Roberts & Sherrat 1998), respectively expecting the duration of bouts to remain relatively short constant or to increase step by step. I also study whether regular or irregular partners influence the bout distribution and I investigate the significance of the initial bout of each session. I expect this bout reflects its initiator's eagerness in investing in the interaction.

In this study my purpose is to offer background information on neutral sessions in which grooming seems only exchanged for grooming. As expected, reciprocal bouts are not given randomly and females tend to maximize their benefits by mostly interacting with females of adjacent ranks, which are normally family members in primates. But more interestingly, I show that females distinguish between social partners with whom they interact frequently from partners with whom they interact infrequently and this study can provide the missing link between grooming as a currency when viewed through the scope of biological market theory and grooming as a mechanism in the formation and maintenance of social bonds when viewed through the scope of behavioural ecology.

In the second study (Chapter 3) I investigate the relationship between grooming and obtaining access to infants in both mangabeys and vervets in the context of biological market theory (Noë & Hammerstein 1994,1995). In primates, young infants are very costly to rear and females are usually limited in their reproductive potential because of the parental investment's costs they need to provide their offspring before being able to have a new one (Andersson 1994). Therefore, alloparental support may help them to increase their fitness as shown by Fairbanks (1990) in vervet monkeys. However, in species in which the hierarchy steepness is strong between females, many studies reported alloparenting situations in which females would end up harming other females' infants (e.g. Maestripieri 1994) because low-ranking females were not able to retrieve their infants in time to nurse them. It is quite commonly assumed that mothers are reticent to allow other females to interact with their infants.

In both mangabeys and vervets, females are intensely attracted by newly-born infants and mothers are shown to allow infant handling after grooming sessions. Following Henzi and Barrett's (2002) idea about grooming being exchanged for infant handling in a biological market context, I first check whether infant access is really a commodity worth trading for. Hence, I expect that the amount of reciprocation within a grooming session really drops with regard to

grooming sessions in which grooming is exchanged for itself and that grooming interactions are immediately followed by infant handling. Secondly, I estimate the value attributed to a newborn. According to females' general attraction for infants I predict that this value is superior to the value attributed to reciprocal grooming and requires longer grooming bouts. Furthermore, I expect that basic market rules such as the supply and demand principle as well as power asymmetries between females affect infant values throughout time. This scenario would be validated if the amount of grooming non-mothers have to give prior to handling infants is influenced by the amount of infants present in the group, by both mothers and non-mothers hierarchical status and even by the infants' age. Indeed, older infants may not be as attractive as newborns. Eventually, I focus on the way non-mothers are allowed to interact with infants. I expect that the time devoted to infant handling is related to the amount of grooming mothers received. It seems difficult to make any predictions about the influence of the infants' age as two contradictory effects simultaneously occur when they are getting older: mothers are less protective but at the same time, infants become less attractive to interact with since their black baby coat is progressively turning into the typical adult coat (grey for mangabeys, beige for vervets). Unfortunately, the reward study can only be performed on vervets.

I find that similarly to previous studies, the mangabey and vervet infant markets are influenced by the number of available infants as well as their value in terms of age and their mother's rank. Contrary to other studies however, I work with a large data set allowing the use of linear mixed effects models. This particular choice of analysis really ascertains the complexity of the market and its many fluctuations. Furthermore, I am the first to study infant handling and find that females also tend to act differently with frequent and infrequent social partners.

In the third study (Chapters 4 and 5) I investigate the mating market in mangabeys. In primates, competition has long been seen as the major force driving their social structure evolution and the reproduction is not exempt of it. In many species, males do not provide much

infant caring and are usually seen as the competitive gender while females are solely exerting mate choice. In female-bonded species however, this reduction of both genders' roles seems to overlook a whole part of the sexual market. The presence of certain males seems to benefit females: in the case of high infanticide risks, putative fathers may protect females and infants from aggressive males (Palombit 1999). Therefore, females' competition over males may be an aspect worth investigating. It is worth noting than in mangabeys, infanticide risk is quite high, despite a multi-male/multi-female social system (van Schaik 2000), with numerous non-resident males entering groups prior to and during the mating season. Females are expected to develop anti-infanticide strategies and I assumed that mothers of young infants would seek the protection of putative fathers. In a first chapter (Chapter 4), I then focus on infanticide risks and how the presence of non-resident males changes many spatial organisations and behaviours among the group members such as the mothers of newborn infants clustering together with no regard to their rank status and the effective protection against infanticide risks from resident males.

In a second chapter (Chapter 5) I study males and females competing for mate access and more particularly, I investigate the way the fluctuating supplies of adult males and receptive females (OSR) influence grooming interactions. During the mating season, mangabey females display exaggerated sexual swellings that give a convenient graded signal to estimate the period when they are sexually receptive (Noë & Sluijter 1995, Nunn 1999) and they are shown to multiply mating, which is thought to confuse paternity (Wolff & Macdonald 2004). I investigate the way receptive females groom resident and non-resident males in order to mate with them. I suspect that such grooming sessions are reciprocated but directly followed by mating and that females' grooming investment varies according to their fluctuating "receptive" value. I also check whether the basic market law of supply and demand influences the grooming duration.

Interestingly, I find that contrary to most other species, mangabey females are the gender seeking for sexual opportunities (see Gomes & Boesch 2009 and Gilby et al. 2010 for another

such exception in chimpanzees). They groom males in order to secure mates. Both males' availability and the number of receptive females influence the market.

In the fourth study (Chapter 6) I test a specific market law in vervet monkeys. By running a market experiment in the field, I investigate the effects of variable ratios of supply and demand on grooming behaviours. To do so, I artificially induce changes in the supply and demand ratio in two wild vervet groups. In the view of some results I found in the first study, a) I chose to work with subordinate females as grooming investment is usually not benefiting them and b) I assumed that my experiments would influence the total amount of grooming sessions very little. In fact, both vervet groups spend about 15% of their daily budget grooming each other and Henzi & Barrett (1999) showed that such a considerable budget would hardly fluctuate across the year even in the face of increased other demands: even when food is scarce, necessarily longer foraging sessions would preferentially be taken on the resting budget rather than on the grooming budget.

To create an artificial market in both groups, I chose first a single and then two low-ranking females as food providers by allowing them to supply apples contained in wooden framed boxes to other group members. I expected that such a setup influences the way grooming is exchanged between these providers and the other group members. Notably, I predicted that the grooming distribution differs in terms of time each partners invests in a grooming bout, i.e. the ratio "grooming time invested by provider – grooming time invested by non provider" eventually benefits the former. More precisely, I predict that the changes in the grooming ratios especially affects the first providers when they are the only one in their respective groups (phase1) and seriously differs from the values recorded during the observational period (non-test phase) that I used as a control phase. I also expect the effect to drop with the appearance of a simultaneous competitive provider (phase2).

In this very first field experiment specifically testing the law of supply and demand in primates, I show that the grooming ratios benefit females as soon as they become providers. The

benefits drop when the second providers are introduced, demonstrating the effect of the law of supply and demand.

In the fifth study (Chapter 7) I investigate the effects of high-ranking individuals' learning to control themselves on the emergence of cooperative interactions. Indeed, in the early stages of my field experiments, high-ranking individuals monopolised the closed containers and prevented the providers from opening them. After a few trials, the time required for providers to open their respective containers significantly dropped along with aggression rates while the distances between each container and the high-ranking partner increased above 10 meters. Hence, I expect that the time required for each provider to open a container is explained by the rates of aggression as well as the duration of the container monopolisation. In a second step, I study the time required for each high-ranking individual to actively leave the close vicinity of the container and wait at more than 10 meters from it. Displayed in chronological order, these timings form temporal curves that convey information about the mechanisms at stake in self-control learning. I expect monkeys to learn individually and in a sequence, i.e. the highest-ranking subject learns first, then the next highest-ranking learns, then the next one until most obstacles for providers to access the container are lifted. This chapter may be the first study to show self-control in wild animals and to give supportive evidence of how queuing-to-learn system may alleviate the social pressures that lay upon complex behaviours such as cooperative interactions.

I show that there is indeed a queuing-to-learn system. Random behaviours at the beginning of the experiment suggest trial-and-error learning mechanisms. However, the acceleration of the pace required for one individual to learn after the previous one had learnt, suggests that social enhancement may play a role as well.

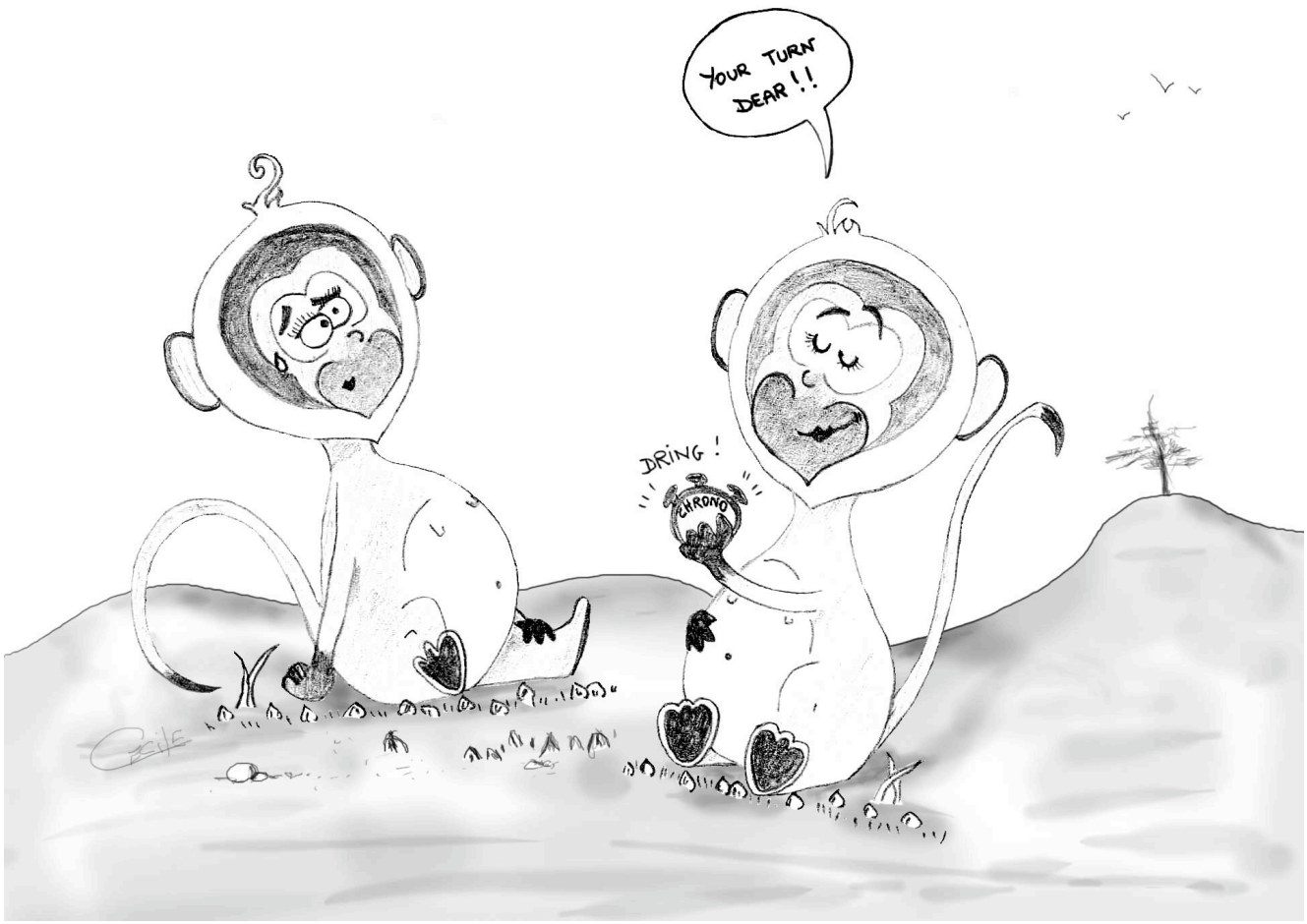
CHAPTER 2

Immediately exchanged grooming bouts in sooty mangabeys and vervet monkeys

A short overview of the potential mechanisms

Cécile Fruteau, Sylvain Lemoine, Eléonore Hellard, Eric van Damme, Ronald Noë

In revision Animal Behaviour



C & JM Fruteau

ABSTRACT

We tested predictions following from the biological market paradigm using reciprocated grooming sessions among the adult females in a sooty mangabey group with 35 females (Ivory Coast) and in two groups of vervet monkeys (South-Africa) with four and seven females, respectively. As expected, females optimized their benefits by frequently grooming closely ranked partners and time matching their exchanges. Such dyads were characterized as frequent grooming partners. Power asymmetry such as female's status in the hierarchy altered their exchanges, the subordinate female of a dyad having to groom longer than her partner. Moreover, the dyadic structure of the grooming sessions allowed us to investigate 'partner control' strategies such as "parcelling" and "raising the stakes". Females of both species neither parcelled nor gradually invested more grooming within sessions. Rather, the longer bouts of a grooming session were usually given at the beginning of the session and we found that the length of the first bout a frequent grooming partner gave her partner at the beginning of a session, predicted the length of the whole session. Furthermore, we investigated the trust building in frequent and infrequent grooming partners. We found that infrequent groomers of both species did not build trust and the first bout they invested in a grooming session could not predict the session length. We conclude that each female has a good knowledge of her value as a grooming partner within each dyad and knows how much she should invest in order to receive grooming within the same session.

Altruistic behaviours, i.e. behaviours that are costly to their donator but beneficial to their receiver at least in the short term, have long been considered as paradoxical in evolutionary terms until Hamilton (1964) and Trivers (1971) provided explanations for their occurrence in related (kin selection theory) and non-related (reciprocal altruism theory) individuals, respectively. However, Trivers' theory, which focuses on partner control within an iterated prisoner's dilemma IPD has proved difficult to demonstrate in nature (e.g. Roberts 1998; Hammerstein 2003; Bshary & Bronstein 2004; Sachs et al. 2004; Bergmüller et al. 2007; Silk 2007; West et al. 2007a; West et al. 2007b but see Bshary et al. 2008 for an illustration of a natural occurrence of IPD) and results of experiments with primates are mixed (e.g. Melis et al. 2008; Brosnan et al. 2009). Biological market theory (Noë & Hammerstein 1994; 1995) proposed another explanation that stresses the importance of partner choice. Following this theory, two partners exchange low cost commodities to their mutual benefit, which switches the interest from demonstrating reciprocated altruistic behaviours to understanding which process rule them. The price invested to obtain the commodity as well as the choice of the best possible partner follow economic rules based mainly on outbidding competition and supply-demand ratios. While many studies in plant/insect, plant/microorganisms systems (e.g. Schwartz & Hoeksema 1998; West et al. 2002) and cleaner fish trades (e.g. Bshary 2001) have shown the importance of the biological market theory in predicting how cooperative behaviours are done, conclusions are still controversial in primates (e.g. Barrett et al. 1999; but see Schino et al. 2003).

In primates, adult allogrooming (grooming, hereafter) has long been considered as an indicator of the quality of the long-term bonds between individuals (Hinde 1976; Schino et al. 2007). More recently and under the scope of the biological market, grooming has been considered as a low-cost positive social currency (Barrett et al. 1999; 2000) whose reciprocation time frame is short-term and whose value is merely functional; i.e. hygienic with the removal of ectoparasites (Hutchins & Barash, 1976; Zamma 2002) and hedonistic with the release of beta-endorphins (Keverne et al. 1989). Hence, given grooming is either immediately reciprocated by the partner

(Barrett et al. 1999; 2000; Manson et al. 2004; but see Schino et al. 2003 for results on long time frame reciprocation) or exchanged for agonistic support (Hemelrijk & Ek 1991; Schino 2007), food (deWaal 1997), access to an infant (Henzi & Barrett 2002; Gumert 2007a; Fruteau et al. accepted) and mate compliance (Gumert 2007b).

In this paper we investigated grooming sessions (hereafter, neutral sessions) that were not exchanged for obvious commodities such as food, infant and mate accesses in two primates species, the sooty mangabeys (*Cercocebus atys*) and the vervet monkeys (*Chlorocebus aethiops*). We defined a grooming session as a sequence of exchanged bouts between two partners. We used the framework of the biological market theory (Noë & Hammerstein 1994, 1995) to investigate how grooming bouts were traded among females. We first checked whether supply/demand ratios or power asymmetries between partners would influence the grooming bout lengths. When grooming is exchanged for grooming, the 1st minute of a bout is worth more than the last in longer bouts. Hence grooming bouts of equal length would be of equivalent value to the receiver. We expected that if females optimise their benefits they would prefer grooming sessions with partners of similar value (see also Seyfarth 1977). We therefore predicted that females of neighbouring rank would time-match their investments in term of grooming duration (e.g. Henzi et al. 2003). We also predicted that power asymmetries such as rank distance between females would influence the grooming lengths. Indeed, dominants have additional commodities (tolerance at food patches, restraint in dyadic conflicts with the subordinate, agonistic support in conflicts) to trade that subordinates cannot offer. Hence we expected the length of time a female grooms another female to be influenced by the power differential, estimated by the rank distance between the two females, i.e. partners rank distances would be correlated to grooming investment discrepancies.

One of the pivotal elements of biological market models is 'partner choice' (Noë & Hammerstein 1994, 1995; Bshary & Noë 2003). According to this vision the dyads within a group are not seen as independent entities, but rather the group is seen as a single 'market' on which the partner behaviour is controlled by partner switching, or the threat of partner switching, rather than

by breaking off the relationship, or the threat of such a 'defection'. However, biological market does not exclude the use of 'partner control' strategies. One such partner control model that would apply to grooming is Connor's parcelling model (1995), which assumes that cooperating individuals are initially caught in an iterated prisoner's dilemma. By delivering their goods and services in small packages they de facto change the payoff matrix of each round of the game in such a way, however, that it is no longer a prisoner's dilemma, and thus reduce the risk of exploitation. The model applies especially well to grooming, since the service can be delivered in packages of almost any size and would predict that grooming bouts remain short within grooming sessions. Here the problem is that we can hardly predict how short a bout should be to fulfil the requirements of the payoff matrix. We therefore reduced our test of this model to testing the simple prediction that grooming partners should take turns within grooming sessions and that the grooming bouts should be roughly equal in length within and between partners.

Roberts & Sherratt (1998) developed the idea of the parcelling strategy further and proposed the 'raising-the-stakes' (RTS) strategy according to which animals can limit the risk of being exploited by starting with delivering small packages, but then increasing the costs of the portion delivered in each round, as long as the partner continues matching the investment. The dyadic structure of grooming sessions makes them likely interactions in which RTS could be used (Keller & Reeve 1998). We looked therefore for the use of RTS within grooming sessions but not over longer series of grooming sessions as Barrett and Henzi (2000), after attempting to compare investments between grooming sessions chronologically dispersed over time in baboons, concluded that one has little chance to record the real starting point of a relationship. If RTS is used, then we expect firstly that partners invest little at the beginning of the session and gradually increase their investment if their partner at least matches the last bout of grooming given. Secondly, we made a distinction between dyads grooming frequently and those grooming infrequently, assuming that trust building would still be necessary in the grooming sessions of the latter. Females are philopatric in both sooty mangabeys and vervets, so we assumed frequent

groomers to be close kin or at least familiar enough with each other at a level that would make trust building superfluous. Hence we predicted frequent grooming partners to groom longer at the start of the session than infrequent groomers do. Thirdly, the first bout of a session may reflect the willingness of the individual to invest in this grooming session. Thus, we predicted that the first grooming bout within a session is longer for frequent partners than for infrequent ones.

METHODS

Research areas, subjects and data collection

Sooty mangabeys

We conducted the study in the Taï National Park, Ivory Coast between November 1, 2001 and August 20, 2002. The park is one of the last remaining blocks of West African primary forest and covers about 454,000 ha. The forest is classified as "tropical moist forest" (Whitmore 1990), with a mean annual rainfall of 1875 mm, a mean annual temperature of 24°C (Taï Monkey Project data, 1991-1999) and a distinct dry season from December to March.

Our group of mangabeys was well habituated to human observers prior to the start of the study and we could recognise all adult, sub-adult and infant members by facial features. Its home range covered about 7 km^2 near the western border of the park. The group was not provisioned. During the study we observed 7-14 adult males, 35 adult females, about 70 juveniles and sub-adults. Seven infants were born between December 10, 2001 and March 10, 2002. One died on February 2, 2002.

We focused the data collection on adult females. We used unidirectional "approach/retreat" and "threat/retreat" interactions to determine the female dominance hierarchy. It remained stable throughout the study period (linearity of the female rank order: MatMan test: $\chi^2_{41} = 447.89$, $p < 0.0001$, $h = 0.97$, $K = 0.97$). We used both *ad libitum* and focal sampling observation techniques (Altmann 1974) to collect data on grooming sessions occurring between all females. When grooming sessions occurred between females and mothers of newborns less

than 3 months old, we recorded whether the female gained access to the infant. Grooming bouts were timed to the nearest 30 seconds. A bout was considered to have ended when either the direction of grooming changed or when there was a break of > 30 sec. We used 15-min focal sampling with at least 60 min between consecutive samples of the same individual and 3 min between samples of different individuals. However, for the analyses we also used the focal samples that were at least 9-min long (89 out of 2272 samples) if they were truncated because the subject moved out of the observer's sight. For each focal animal, we recorded each minute on the minute (instantaneous sampling, Altmann 1974): the infant's presence / absence, distance from the mother and the nearest adult female and adult male within 5 meters. Social interactions were recorded continuously (detailed ethogram in Range & Noë 2002). Due to limited visibility in the early evening, we opted for a sampling schedule from 7:00 to 16:00. We collected a total of 568 hours of focal samples for all of the 35 adult females (ranging from 63 to 65 per female). All females were followed at least once every three days and we randomized each female's sampling to account for the time of day. *Ad libitum* data were recorded all day long (even while doing focal sampling on a subject) as soon as a social interaction (aggression, grooming, mount, etc.) between two identified individuals was observed.

Vervet monkeys

We conducted the study in the Loskop Dam Nature Reserve, Mpumalanga province, South Africa. The Loskop reserve is characterized by a 'bushveld' (tall grasses, thick acacia bushes) type of habitat. The reserve covers approximately 25000 ha, on average 1000 m above sea level. The area has dry and cold winters (temperatures below 5°C at night and 25°C during the day) from May to October and hot and humid summers (rainfalls of about 500mm; temperatures ranging from 25°C to 40°C) from November to April.

Both study groups had home ranges of approximately 3 km^2 each that were about 3 km apart. The home range of the Donga group was following narrow dried river beds and mainly

contained tall trees such as fig trees while the home range of the Picnic group was situated in a plain essentially composed of tall grasses and acacia bushes. An artificial lake provided water to the group the whole year round. The Donga group did not have contacts with tourists and was not provisioned outside the context of experiments (see Fruteau et al. 2009). The Picnic group was provisioned by tourists, almost exclusively on Sundays, and regularly ate from the dustbins of the picnic site. The group also obtained food awards during experiments (see Fruteau et al. 2009). The Donga group was habituated to the presence of human observers at the beginning of the study (from May to mid-October 2004) and the Picnic group was habituated before the second field session (from February to July 2005). The Donga group had three to five adult males, seven adult females, one to two sub adult males and one to two infants at a time. The female dominance hierarchy changed between the first and the second field period after the death of the beta female (linearity of the female rank order: MatMan test: first period: $\chi^2_{23} = 48$, $p = 0.0017$, $h = 1$, $K = 1$; second and third periods: $\chi^2_{20} = 60.67$, $p < 0.0001$, $h = 1$, $K = 1$). The Picnic group had two to three adult males, four adult females, one juvenile male and two to six infants at a time. The female hierarchy stayed stable throughout the two field periods (linearity of the female rank order: MatMan test: χ^2_{undef} = undefined, $p = 0.373$, $h = 1$, $K = 1$).

During the first field period, we followed the Donga group on a regular basis from mid October to mid December 2004. Thereafter, we followed each group every second day during the second field period from September 2005 to the end of April 2006 and two days in a row every four days during the last field period from May 2006 to the end of September 2006. Observations were distributed throughout the day but the majority of the data was taken from 06:00 – 13:00 and from 14:00 – 18:00. Data were collected by focal group sampling of the adult animals (Altmann 1974), i.e. when all adults were visible simultaneously, or by *ad libitum* sampling when only one observer was in the field or when one adult animal was out-of-sight or missing from the group. The data represent for the Donga and Picnic groups 605 and 422 hours of group focal and 100 and 70 hours of *ad libitum* sampling, respectively. Grooming bouts were timed to the nearest second.

A bout was considered to have ended when either the direction of grooming changed or when there was a break of > 20 sec.

Data analysis and statistics

For this study, we excluded all grooming sessions including juveniles, males, mothers of infants of less than three months old and receptive females. In vervets we also discarded the grooming sessions taking place during our experimental periods. As we observed two vervet groups, whenever the same effects were found in both groups we gave combined probabilities following the formula $\chi^2_{df} = - 2 \Sigma \ln P$ with 4 degrees of freedom (Sokal & Rohlf 1995). Tests were performed using SPSS (version 17.0) and R (version 2.10.1). The alpha-level was set to 0.05.

We first studied general descriptive statistics of these reciprocated grooming sessions for both species: daily budget, average grooming session length, time lag between a bout and its reciprocation. We used a two-tailed G test to compare the proportion of initiations performed by the lower-ranking females of a dyad with the expected value assuming no effect of status.

We then tested whether females tended to time-match their exchanges or were influenced by their partner's status, using simple linear regressions. We transformed the data following the method proposed by Manson and collaborators (2004): we weighted the contribution of all data points and standardized them by subtracting the mean and dividing by the standard deviation. This allowed the use of all grooming sessions while ensuring that they could be considered as independent and that each cluster equally contributed to the test. We regressed the time invested by receivers on time invested by initiators to test whether females time-matched their grooming bouts in the course of a session and we regressed the rank distances on time discrepancies to test whether their respective status influenced their investment.

Finally, to test whether females would use either parcelling or RTS, we followed the method proposed by Barrett & Henzi (2000). We used all grooming sessions containing at least three bouts. We assigned a minus sign to bouts that were shorter than the previous bout and a plus

sign to bouts that were either longer or equivalent. Using Sign tests we tested: (a) whether bout lengths increased, or remained constant, over the whole grooming session irrespective of the groomer (between partner test) and (b) whether they increased, or remained constant, for each of the partners separately (within partner test). We used a non-parametric two-way Friedman ANOVA to test whether the grooming bout lengths would change over the full study period. To compare frequent grooming partners with infrequent ones, we used the criterion proposed by Barrett & Henzi (2000): groomers were frequent partners if they spent more than 5% of their total active (when the individual does groom) + passive (when the individual is groomed) grooming time grooming each other. We used two-tailed Mann-Whitney-U tests and Spearman correlations to test the predicted differences between frequent and infrequent partners.

RESULTS

Pattern of grooming sessions

The daily budget and the average session length data are summarized in Table 1. In the mangabeys 355 sessions out of 363 (97.8 %) showed grooming in both directions suggesting reciprocation over short time frames. The lower-ranking female initiated 199 of these 355 sessions, which is not a significant deviation from the null-hypothesis of balanced initiative taking (two-tailed G test G1 = 2.374, p = 0.1933).

Groups	**Mangabey**	**Vervet Donga**	**Vervet Picnic**
Size	≈130	≈15	≈11
Nb of females	35	7	4
Nb of grooming sessions	363	323	
Nb of non-reciprocated sessions	8	31	
Dailey budget	15.61±1.03 %	15.30±1.08 %	
Average session length	343±129 s	323±325 s	

Table 1 - Grooming pattern in mangabeys and vervets

A comparably high proportion of grooming session in the vervets (292 out of 323; 90.4 %) also showed two-way grooming. However, the lower-ranking females initiated 262 sessions,

which was significantly more often than the number initiated by their higher-ranking partners (two-tailed G test combined probabilities $\chi^2_4 = 15.436$, $p < 0.01$).

Time matching and influence of hierarchy

Both species showed time matching of grooming bouts within sessions, as revealed by linear regressions (mangabeys: $F = 102.062$, $p < 0.0001$; vervets combined probabilities: $\chi 24 = 29.459$, $p < 0.0001$).

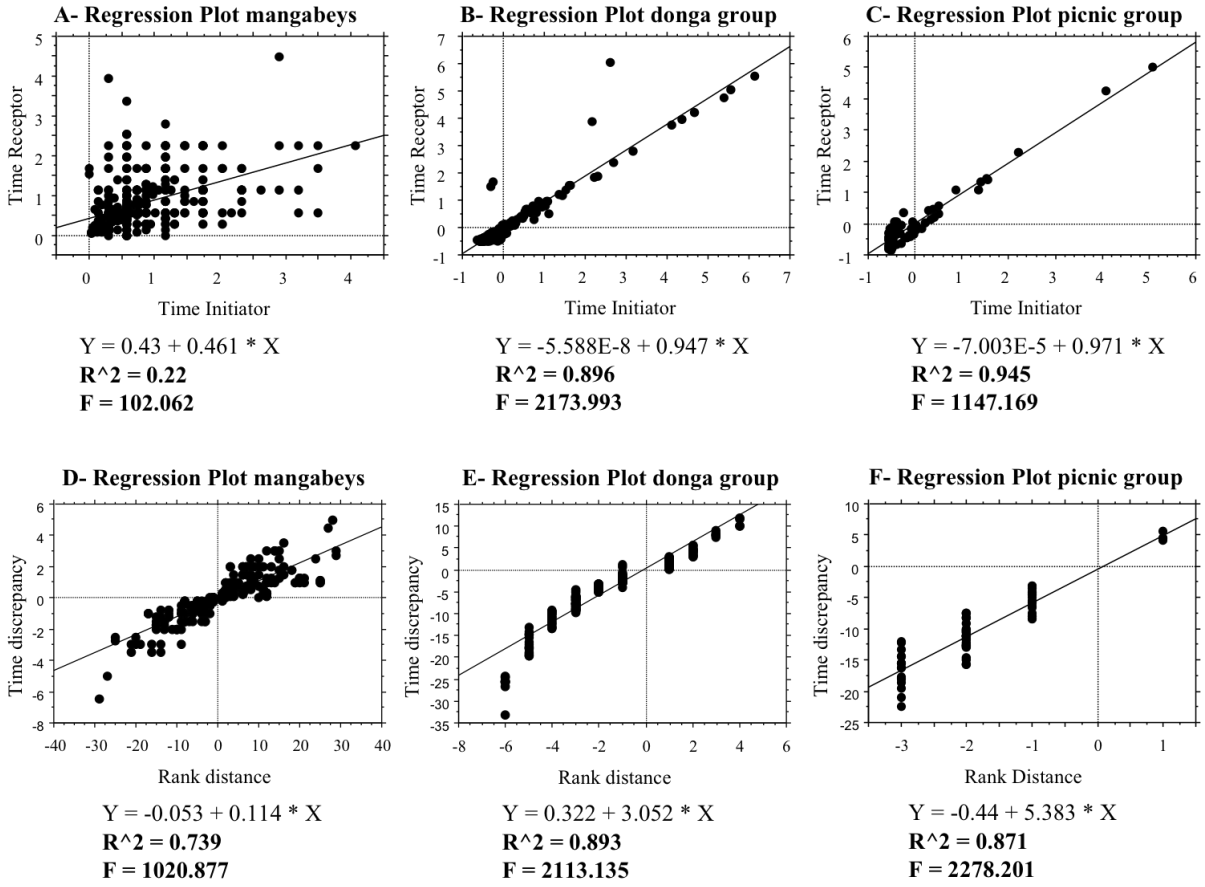


Figure 1. Linear regression plots and equations for Time matching (A in mangabeys, B in vervet Donga group, C in vervet Picnic group) and Influence of status (C in mangabeys, D in vervet Donga group, E in vervet Picnic group). Time discrepancies: Td = time invested by the receiver – time invested by the initiator. Rank distances: Rd = rank of the receiver – rank of the initiator. The data set was transformed in order to perform the regression (weighted and standardized). Therefore axes such as Time Receptor, Time Initiator and Time discrepancy do not have units. The standardization also led to some numbers being negative.

The mangabeys matched the bout length of their partners only to a low degree ($r^2 = 0.22$; Fig. 1A), while the bout length in vervets could be explained much better (almost 90% and almost 95 % respectively; $r^2_{Donga} = 0.896$ and $r^2_{Picnic} = 0.945$; Fig. 1B,C) by time matching Hence, time matching did not seem to play a major role in mangabeys. Note, however, that this result, as well as the next one, is partially explained by the fact that we a priori excluded sessions with a single groomer.

For both species, linear regressions showed a significant and positive rank distance effect on time discrepancy within sessions (mangabeys: $F = 1020.877$, $p < 0.0001$; vervets combined probabilities: $\chi^2_4 = 30.774$, $p < 0.0001$), which meant that the lower ranking female of a grooming dyad invested more grooming time than her partner. Rank distances explained up to 74% of the variation observed in time investments ($r^2 = 0.739$; Fig. 1D) in mangabeys and up to 89% and 87% in vervets (respectively, Donga group: $r^2 = 0.893$ and Picnic group: $r^2 = 0.871$; Fig. 1E,F).

Partner control strategies

Group	Nb of bouts (nb dyads)	Increase across session	Decrease across session	Sign test P	Friedman ANOVA test χ^2	df	P
Mangabey	3 (105)	25	80	< 0.0001	67.126	2	< 0.0001
	4 (74)	26	48	< 0.0001	95.967	3	< 0.0001
	5 (82)	16	66	< 0.0001	204.248	4	< 0.0001
	6 (43)	11	32	< 0.0001	113.744	5	< 0.0001
Vervet	3 (111)	17	94	< 0.0001	50.213	2	< 0.0001
	4 (44)	19	25	0.30	64.377	3	< 0.0001
combined	5 (101)	28	73	< 0.0001	199.453	4	< 0.0001
probabilities	6 (15)	8	7	> 0.9999	24.066	5	< 0.0001

Table 2[2] - Parcelling and raising the stakes strategies: evolution of the length of grooming bouts within sessions (Sign test) and across grooming sessions (Friedman ANOVA test)

[2] Are only represented the categories of grooming sessions that contained at least three bouts and five pairs. For the vervet monkeys, the given probabilities are combined probabilities for the two groups. All tests are two-tailed.

For both species the only significant results for the development of the length of grooming bouts found within sessions (analysed using Sign tests) showed a decrease of the grooming bouts lengths within the grooming sessions (Table 2). This is in contradiction with the parcelling model according to which bouts should have remained of similar length throughout the session and opposite to the predictions of the RTS model according to which females should gradually increase their investment in grooming time in answer to their partners' actions. Furthermore, the Friedman tests revealed that there were significant bout length differences across sessions (Table 2), which was also in contradiction to both models.

For both species, the significant results for the evolution of within partner's bout length within grooming sessions (Sign tests for initiators and receivers) showed a decrease of the lengths for both partners (Table 3), which meant that females, contrary to predictions, neither kept the length of their own bouts constant (parcelling) nor increased their length (RTS) within sessions.

Group	**Nb of bouts** (nb dyads)	**Increase initiator**	**Decrease initiator**	**Sign test P**	**Increase receptor**	**Decrease receptor**	**Sign test P**
Mangabey	3 (105)	19	86	< 0.0001	0	105	< 0.0001
	4 (74)	11	63	< 0.0001	6	68	< 0.0001
	5 (82)	9	73	< 0.0001	11	71	< 0.0001
	6 (43)	0	43	< 0.0001	0	43	< 0.0001
Vervet	3 (111)	15	96	< 0.0001	0	105	< 0.0001
	4 (44)	3	41	< 0.0001	1	43	< 0.0001
combined	5 (101)	10	91	< 0.0001	12	89	< 0.0001
probabilities	6 (15)	3	12	0.03	1	14	< 0.001

Table 3[1] – Parcelling and raising the stakes strategies: evolution of the grooming length for each partner's contribution within grooming sessions (Sign tests for initiators and receivers)

Frequent and infrequent grooming partners

In both species, females frequently groomed from two to four females (mangabeys: N = 3.79 ± 1.09 frequent partners; vervets: Donga: N = 3.75 ± 1.04 frequent partners and Picnic: N = 2.04 ± 0.54 frequent partners). The relation was not always symmetric in mangabeys (a partner A could

be frequent for B but B could be infrequent for A) even though it happened for only 4 females. The relation was symmetric in vervet. Frequent partners were significantly closer in rank than infrequent partners were (mangabeys: two tailed Mann-Whitney-U test: U = 4084.5, N1 = 83, N2 = 221, $p < 0.01$; vervets combined probabilities: $\chi^2_4 = 32.236$, $p < 0.01$, N1 = 211, N2 = 112; Fig.2A). For both species and contrary to our predictions a) frequent and infrequent grooming partners invested similar grooming durations for their first bout (mangabeys: two tailed Mann-Whitney-U test: U = 8125.5, N1 = 83, N2 = 221, $p = 0.113$; vervets combined probabilities: $\chi^2_4 = 1.719$, $p > 0.750$, N1 = 211, N2 = 112; Fig.2B) and b) infrequent groomers did invest in significantly longer grooming session than frequent groomers did (mangabeys: two tailed Mann-Whitney-U test: U = 5799.5, N1 = 83, N2 = 221, $p = 0.018$; vervets combined probabilities: $\chi^2_4 = 13.152$, $p < 0.01$, N1 = 211, N2 = 112; Fig. 2C).

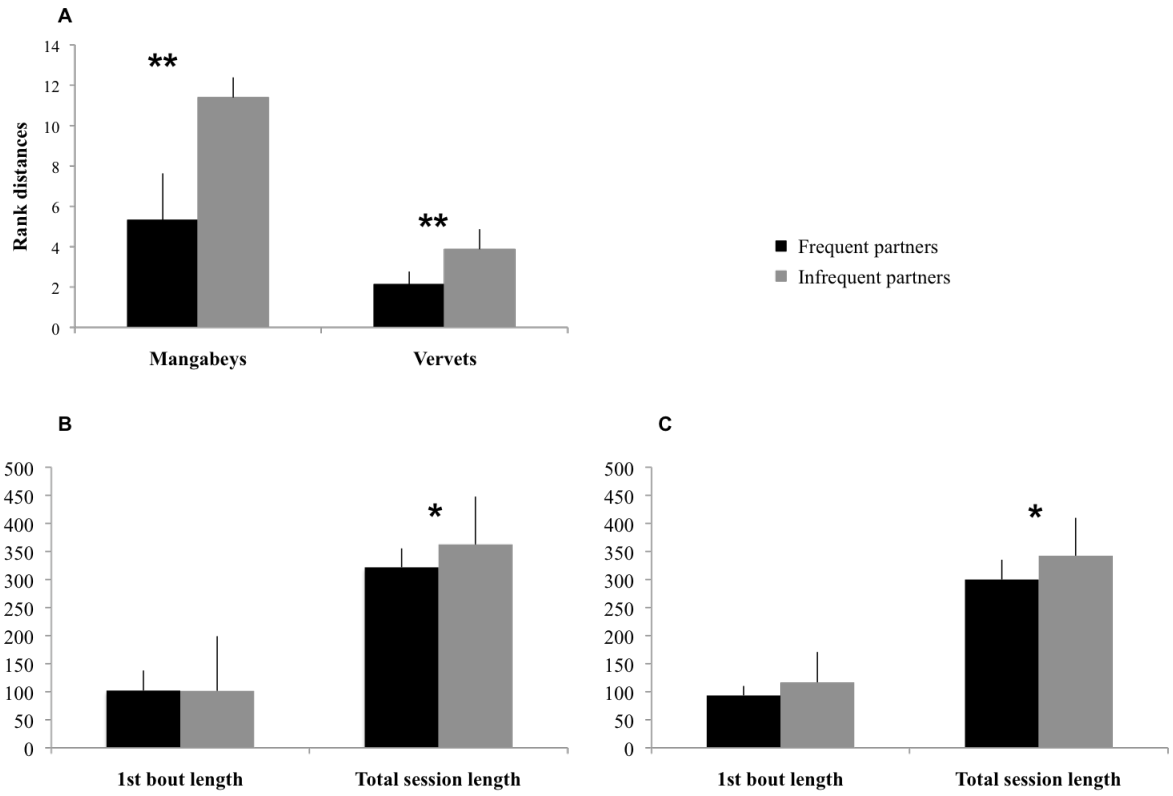
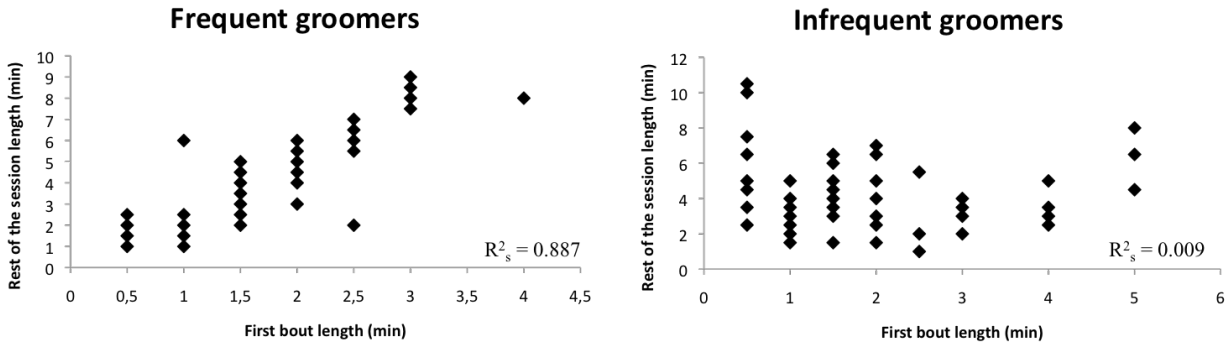


Figure 2. A- Comparison of frequent and infrequent partners' average rank distances. Comparison of first bout length and total session length between frequent and infrequent grooming partners B- in mangabeys and C- in vervets. Mann-Whitney tests are two-tailed; * represents $p < 0.01$ and ** $p < 0.001$.

The Spearman correlations revealed that in both species the initial bout of frequent groomers was significantly and positively correlated to the length of the rest of the session (mangabey frequent groomers: $r_s^2 = 0.887$, $p < 0.0001$; vervets: $r_s^2 = 0.920$, $p < 0.0001$). This contrasted with the lack of significance of the first bout initiated by infrequent groomers of both species (mangabeys infrequent groomers: $r_s^2 = 0.009$, $p = 0.938$; vervets: $r_s^2 = 0.066$, $p = 0.492$; Fig.3).

A- Spearman correlation plots for mangabeys



B- Spearman correlation plots for vervets

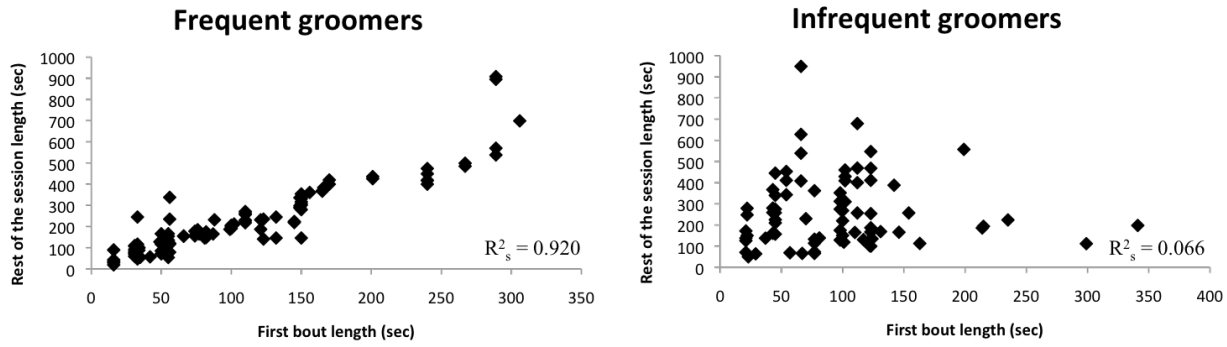


Figure 3. Spearman correlation plots for mangabeys and vervets.

It is to note that the genetic results we gathered in vervets revealed that none of the females from the Picnic group were affiliated. In the Donga group, we singularized two matrilines whose females were of adjacent ranks (first matriline: rank 1, 2, 3 and 4; second matriline: rank 5, 6 and

7). However, the genetic relatedness would not really follow the variable frequent-infrequent groomer (Mann-Whitney-U test: 5 = 15.0, p = 0.055).

DISCUSSION

Both mangabey and vervet females allotted about 15% of their daily budget to grooming with an average session length above five minutes. These first results seemed both surprising and expected; surprising because mangabey females have so many partners to choose from compared to vervet females; and expected because both species have limited time available for grooming in face of other needs such as foraging or vigilance towards predators. A closer look at how females exchanged grooming revealed that most of them had preferred partners with which they spent a disproportional amount of their grooming time. On average, for both species, each female had about two to four frequent partners. In accordance with the biological market predictions and in order to minimize the power asymmetries, these frequent partners were significantly closer in rank than infrequent ones and generally tended to time match their grooming bouts within sessions. Indeed, when we used all grooming sessions occurring in each group, regressions revealed a stronger time matching effect in small vervet groups than in large mangabey groups: in mangabeys frequent groomers were diluted among infrequent groomers, which led to a poor coefficient of regression (0.22) while in vervets, most females were frequent groomers. While we did not have the genetic relatedness of the mangabey females, we found that in the Donga group, vervet females of adjacent rank belonged to the same matriline, while in the Picnic group, none of the females were affiliated. In the Donga group however, affiliation could not really predict whether females were frequent or infrequent groomers.

If females usually tended to optimize their benefits by interacting with closely ranked partners, their status in the group significantly affected their respective investments as predicted by the biological market theory. Regressions analyses showed that females' rank distances were correlated with their investment discrepancies: in both species the subordinate female of a dyad

groomed her partner significantly longer than she was groomed in return. However, we would have expected the effect to be stronger in large mangabey groups than in small vervet groups as in mangabeys the power asymmetries in term of rank distances are larger (± 34) than in vervets (± 6 or ± 3). We can only guess that the dominance relationship between two females does not necessarily say much about the value of tolerance and support in a group. In fact, the value of tolerance may depend on the possibilities of monopolizing food patches and may even vary with the personalities (bold, shy, aggressive, tolerant, etc.) of the dominant individuals (e.g. Itoh 2002) and support may vary according to the rate of conflicts occurring within the group. As for power differentials, they may depend on the steepness of the rank order in each species. In this sense, it is interesting that in mangabeys both low and high-ranking partners initiated grooming sessions, suggesting a more egalitarian social system, while in vervets most of the interactions were started by the lower-ranking partner /member of the dyad.

Our search for possible partner control strategies revealed that both sooty mangabeys and vervet monkeys either failed to parcel (in the sense of the parcelling model) or to raise the stakes either in answer to their partners' grooming investment or to their own previous investment. Instead, our results, as far as statistically significant, showed that females invested in longer bouts at the beginning of the sessions, which is in contradiction to exploitation prevention or trust building. In species such as mangabeys and vervets, in which females have well-established relationships, trust building may not be apparent over short time frames such as single grooming sessions. As it also seemed trivial to to test trust building on longer time frames since it was impossible to appraise when a relationship did start (see Barrett and Henzi 2000), we conclude that even such an easy notion like the establishment of trust may be rather difficult to record in nature and that the mechanisms motivating dyadic relationships such as grooming are hardly explained by simple notions.

We therefore chose another approach by analysing the difference between frequent and infrequent grooming partners. Contrary to predictions, infrequent groomers, between whom trust

building may not have been already completed, did not invest in initial grooming bouts that were shorter than frequent groomers. However, the first bout they gave at the beginning of a session could not predict the length of the session. In contrast, the first invested bout in frequent groomers predicted the length of the session. Its length was directly correlated to the length of the rest of the grooming session and long first bouts predicting long sessions. If this finding does not directly demonstrate trust building, it still shows that females have a good knowledge of the quality of their relationships with others and may give some cues on how females choose between partners. Biological market main control mechanism is to switch partner and the 'playing off partners' predicts that animals base their preferences on past experiences with multiple partners that reach back deeper in the past than either parcelling or RTS (see Schino & Pellegrini 2009 for attitudinal bookkeeping or Fruteau et al. 2009 for attitudinal partner choice). This very first bout seems to give both partners an indication of the quality of the interaction that follows. It may also be a means to quickly negotiate the terms of the interaction by making a first bid. It would have been interesting to investigate this further by testing whether the length of the first bout also predicts whether the partner would reciprocate at all. Unfortunately, for both species, we had too few non-reciprocated bouts to run the necessary logistic regressions.

To summarize, in both mangabeys and vervets neutral dyadic grooming sessions exchanged between females showed that grooming was mainly traded for itself on a short time frame, which supports the 'low cost positive social currency based on short term causal relationships' introduced by Barrett and collaborators (1999). However, grooming was also strongly affected by dominance, partner choice and whether individuals were frequent or infrequent partners, which supports the idea of the knowledge of long-term relationships between partners (Seyfarth & Cheney 1984). We can conclude that grooming is an exchangeable commodity whose value can fluctuate according to both short term and long term relationships existing among all the partners composing the market.

ACKOWLEDGEMENTS

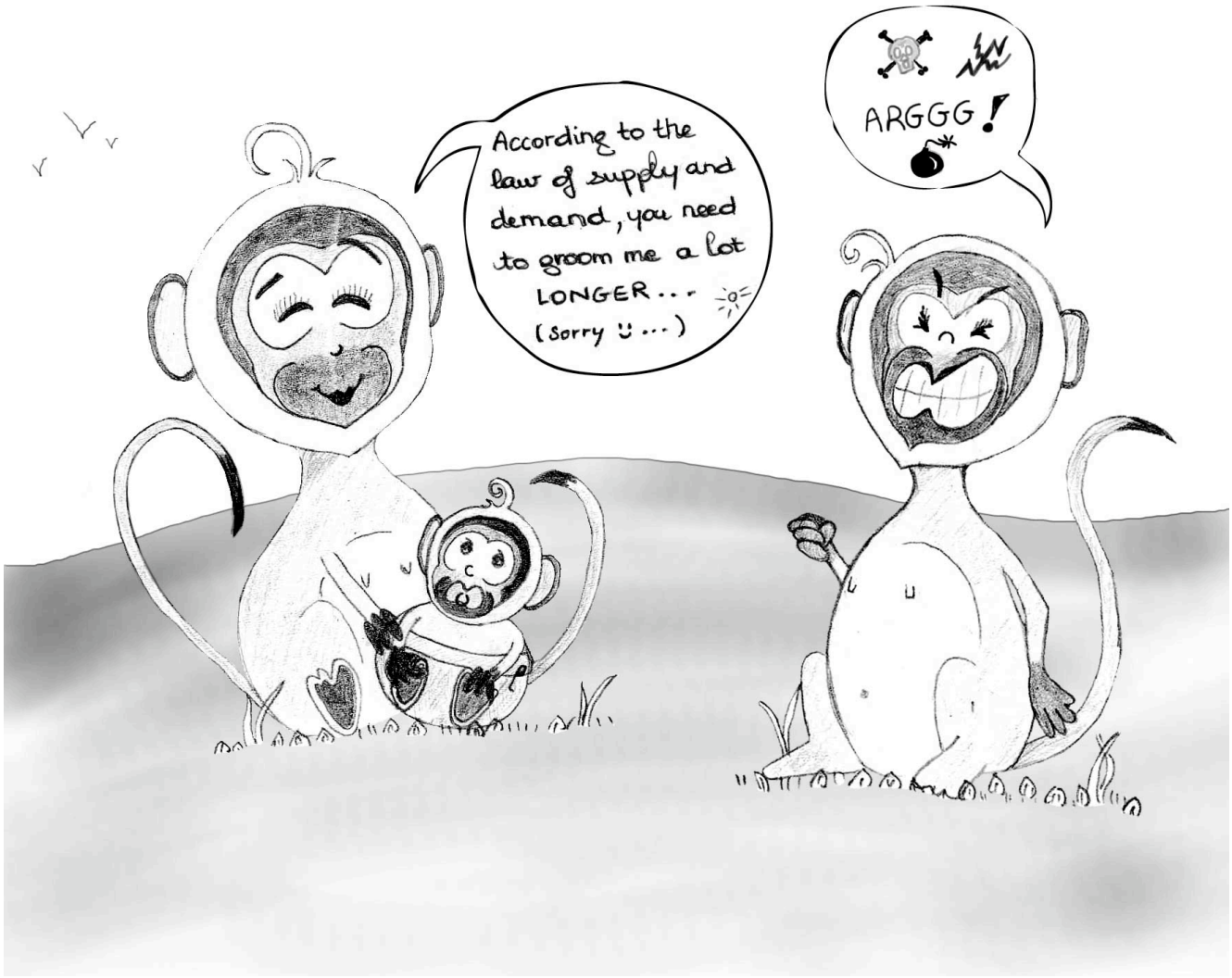
We thank the Ministère de la Recherche Scientifique, the Ministère de l'Agriculture et des Ressources Animales, the CSRS, the CRE and the Taï Monkey Project in Ivory Coast and the Mpumalanga Parks Board, UNISA and ABEERU colleagues, L. Brown, L. Barrett, S. P. Henzi and R. Bshary in South Africa for research permission and logistic support. We thank G. Gha, R. Peho and F. Range in Ivory Coast and S. Aubel, A. Barrett, A. Brotz, D. Carter, V. Dufour and E. van de Waal in South Africa for assistance in the field. We thank N. Poulin for statistical advice. Max-Planck-Institut fuer Verhaltensphysiologie, CNRS and NWO (Evolution and Behaviour 051-12-036) provided financial support.

CHAPTER 3

Infant access and handling
Baby Market in Sooty Mangabeys and Vervet Monkeys

Cécile Fruteau, Erica van de Waal, Eric van Damme, Ronald Noë

Accepted in Animal Behaviour



C & JM Fruteau

ABSTRACT

Access to one's newborn infant is a commodity that can be traded for other benefits such as grooming in nonhuman primates. According to the biological market paradigm, the price paid should fluctuate with the number of newborns in the group. We investigated the grooming sessions between mothers with infants less than 3 months old and other adult females in free-ranging primates: one group of sooty mangabeys, *Cercocebus atys*, with 35 adult females (Ivory Coast) and two groups of vervet monkeys, *Chlorocebus aethiops*, with four and seven females, respectively (South Africa). Although many more infants were born per birth season in the mangabey group than in the vervet groups, interaction patterns involving infants showed many similarities: mothers did not reciprocate grooming received from nonmothers, but exchanged it directly for the opportunity to handle their infants, whereby obtaining access to infants required longer grooming bouts than reciprocating grooming in grooming sessions not involving infants. Low-ranking handlers needed to groom mothers for longer than their higher-ranking counterparts. The 'value' of an infant, in terms of grooming time received by the mother, decreased when infants grew older or when many infants were simultaneously present in the group. In vervets, infant availability affected handling times: females handled infants for longer when there were fewer infants. Furthermore, only frequent grooming partners of the mother could handle infants for longer and this familiarity was not kin related. This suggests that if the value of an infant varies with dominance, infant handling time may be determined by the quality of the females' relationships.

Newborn infants attract a lot of attention from other members of primate groups and notably from females. Mothers carrying newborns are often approached by females that try to touch, handle and inspect their infants. Before gaining access to the infant, would-be handlers often have to groom the mother (Muroyama 1994). There has been considerable discussion about the function of infant handling (Lancaster 1971; Hrdy 1976; Manson 1999; Silk 1999), but what interests us in this study is the amount of grooming that has to be 'paid' before the mother grants access to her infant. This question has gained attention after Barrett & Henzi (2002) characterized the exchange of access to infants for grooming as a trade of commodities in the framework of biological market theory (Noë & Hammerstein 1994, 1995). 'Baby markets' have all the characteristics of a biological market with two classes of traders exchanging commodities that cannot be appropriated by force and a fluctuating supply–demand ratio owing to variation in the number of newborns that attract the attention of their group members. Barrett & Henzi (2002) showed that mothers were groomed for longer when there are fewer newborns in the group, a finding subsequently confirmed in some subsequent studies (Gumert 2007a; Slater et al. 2007), but not others (Frank & Silk 2009; Tiddi et al. 2010).

The baby market studies form part of a much larger set of studies that used biological market theory (henceforth referred to as BMT) to explain grooming patterns in nonhuman primates (Barrett et al. 1999; Payne et al. 2003; Lazaro-Perea et al. 2004; Barrett & Henzi 2006; Gumert 2007b; Löttker et al. 2007; Slater et al. 2007; Chancellor & Isbell 2009; Fruteau et al. 2009; Ginther & Snowdon 2009; Norscia et al. 2009; Port et al. 2009) and other species (Stopka & Macdonald 1999; Radford & Du Plessis 2006; Kutsukake & Clutton-Brock 2010). Other successful applications of BMT to explain intraspecific cooperation patterns include, for example, mating markets in humans (Pawlowski & Dunbar 1999; Pollet & Nettle 2008, 2009) and birds (Greene et al. 2000; Metz et al. 2007; Holveck & Riebel 2010), cooperative breeding and coalition formation in carnivores (Smith et al. 2007; Kutsukake & Clutton-Brock 2008) and labour markets in humans (Macfarlan 2010). Valid examples of biological markets are also found in mutualistic

interactions between members of different species, such as cleaner fish and shrimps and their clients (Bshary 2001; Bshary & Noë 2003; Soares et al. 2008; Adam 2010; Chapuis & Bshary 2010), ants providing protection in exchange for food (Leimar & Axén 1993; Bronstein 1998; Edwards et al. 2006), interspecific nutrient exchanges (Schwartz & Hoeksema 1998; Kummel & Salant 2006; Simms 2006; Heath & Tiffin 2009; Gubry-Rangin et al. 2010) and nursery pollinator mutualisms (Holland 2002; Segraves et al. 2005).

The question why females are so eager to handle infants has been discussed for decades without arriving at a generally accepted conclusion. The interest in handling infants has been explained as 'learning to mother' (Lancaster 1971), reproductive competition through negative consequences for the infant (Hrdy 1976, 1978; Silk 1980; Thierry & Anderson 1986; Maestripieri 1994), a reward for support in agonistic interactions (Manson 1999) as well as a by-product of selection for maternal behaviour (Thierry & Anderson 1986; Clarke et al. 1998; Silk 1999). The opposite question is why females allow others to handle their infants. Primate infants ask for a considerable investment in food, transport and protection (Altmann 1980). Other females can be of considerable help to mothers in this respect (Goldizen 1987; Garber 1997; Silk et al. 2003) and even cause a shortening of the female's interbirth interval in vervet monkeys, *Chlorocebus aethiops* (Fairbanks 1990).

Similarly, there is no consensus about why primates groom each other. There is little doubt that the original function of grooming lies in the removal of ectoparasites and debris in the fur (Hutchins & Barash 1976; Dunbar 1991; Zamma 2002). Primates tend to groom body parts that their partners cannot easily reach themselves (Barton 1985; Borries 1992). However, it looks as if the mechanisms that evolved to make the animals enjoy being groomed, such as the release of certain neurotransmitters (Keverne 1989), became rewarding by themselves and its hygienic function only partially explains grooming patterns (Perez & Baro 1999; Perez & Vea 2000). In any case, primates devote up to 20% of their daily time budget to allogrooming sessions, conserving grooming time even during times of food scarcity (Dunbar 1988, 1992; Dunbar &

Dunbar 1988; Henzi & Barrett 1999) and do not necessarily restrict themselves to those body parts that their partners cannot groom themselves (Perez & Vea 2000; Lewis 2010).

Nonmothers were seen to groom mothers intensely prior to being allowed any direct interactions with their infants in our study groups of sooty mangabeys, *Cercocebus atys,* in Ivory Coast and vervet monkeys in South Africa, which presented a perfect set-up for investigating the 'infant market' in these two species. In a first step, we were interested in knowing whether access to infants was really a commodity with fluctuating value. Keeping in mind that rank usually plays a role in grooming markets as dominants have additional commodities (e.g. tolerance at food patches, restraint in dyadic conflicts with the subordinate or even agonistic support in conflicts) to trade that subordinates cannot offer, we expected the length of time a female groomed another female to be influenced by (1) the fact that this female was a mother, (2) the power differential, estimated by the rank distance between the two females, (3) the number of infants in the group and (4) the infant's age. We tested the following hypotheses.

H_1: Mothers are more attractive than nonmothers. Hence, females groom mothers for longer than nonmothers.

H_2: The subordinate of a dyad grooms more than the dominant as long as their 'motherhood' status is the same, that is, if they have no infants or infants of approximately the same age.

H_3: Females groom mothers for longer when infants are scarcer.

H_4: Females groom mothers for longer when their infants are younger.

In a second step we investigated infant handling time. We expected the time that females spent handling infants to be directly related to the time they spent grooming their mothers. Our hypotheses were the following.

H_5: Handling length is positively correlated with grooming length.

H_6: Females are allowed to handle infants for longer when they dominate mothers.

It was difficult to make any predictions about the influence of the infant's age as two contradictory effects could simultaneously occur: when infants get older (1) they may be less attractive and (2) their mothers may be less protective.

METHODS

Research areas, subjects and data collection

Sooty mangabeys

We conducted the study in the Taï National Park, Ivory Coast between 1 November 2001 and 20 August 2002. The park is one of the last remaining blocks of West African primary forest and covers about 454 000 ha. The forest is classified as 'tropical moist forest' (Whitmore 1990), with a mean annual rainfall of 1875 mm, a mean annual temperature of 24 °C (Taï Monkey Project data, 1991–1999) and a distinct dry season from December to March.

Our group of mangabeys was well habituated to human observers before the study and we could recognize all adult, subadult and infant members by facial features. Its home range covered about 7 km^2 near the western border of the park and was essentially composed of marshes with thick bushes and forest. The group was not provisioned. During the study we observed 7–14 adult males, 35 adult females, about 70 juveniles and subadults. Seven infants were born between 10 December 2001 and 10 March 2002. One died on 2 February 2002. The six surviving infants started to interact directly with group members other than their mothers when they were 3 months old. At least 21 juveniles born during the previous years were still regularly suckling at the beginning of the study: 13 of them stopped when they were about 12 months old and the rest carried on until after they were 18 months old.

We focused the data collection on adult females. We used unidirectional 'approach/retreat' and 'threat/retreat' interactions to determine the female dominance hierarchy. It remained stable throughout the study period (linearity of the female rank order: MatMan test: $\chi^2_{41} = 447.89$, $P < 0.0001$, $h = 0.97$, $K = 0.97$). We used both ad libitum and focal sampling observation techniques

(Altmann 1974) to collect data on grooming sessions occurring between all females. When grooming sessions occurred between females and mothers of newborns less than 3 months old, we recorded whether the female gained access to the infant. Grooming bouts were timed to the nearest 30 s. A bout was considered to have ended when either the direction of grooming changed or when there was a break of > 30 s. We used 15 min focal sampling with at least 60 min between consecutive samples of the same individual and 3 min between samples of different individuals. However, for the analyses we also used the focal samples that were at least 9 min long (89 of 2272 samples) if they were truncated because the subject moved out of the observer's sight. For each focal animal, we recorded each minute on the minute (instantaneous sampling, Altmann 1974): the infant's presence/absence, distance from the mother and the nearest adult female and adult male within 5 m. Social interactions were recorded continuously (detailed ethogram in Range & Noë 2002). Owing to limited visibility in the early evening, we opted for a sampling schedule from 0700 to 1600 hours. We collected a total of 568 h of focal samples for all of the 35 adult females (range 63 - 65 per female). All females were followed at least once every 3 days and we randomized each female's sampling to account for the time of day. Ad libitum data were recorded all day long (even while doing focal sampling on a subject) as soon as a social interaction (aggression, grooming, mount, etc.) between two identified individuals was observed.

Vervet monkeys

We conducted the study in the Loskop Dam Nature Reserve, Mpumalanga province, South Africa. The Loskop reserve is characterized by a 'bushveld' (tall grasses, thick acacia bushes) type of habitat. The reserve covers approximately 25 000 ha, on average 1000 m above sea level. The area has dry and cold winters (temperatures below 5 °C at night and 25 °C during the day) from May to October and hot and humid summers (rainfall about 500 mm; temperature 25 – 40 °C) from November to April.

Both study groups had home ranges of approximately 3 km^2 each that were about 3 km apart. The home range of the Donga group followed narrow rifts and mainly contained tall trees such as fig trees, while the home range of the Picnic group was situated in a plain essentially composed of tall grasses and acacia bushes. An artificial lake provided water to the group the whole year round. The Donga group did not have contact with tourists and was not provisioned outside the context of experiments (see Fruteau et al. 2009). The Picnic group was provisioned by tourists, almost exclusively on Sundays, and regularly ate from the dustbins of the picnic site. The group also obtained food rewards during experiments (see Fruteau et al. 2009). The Donga group was habituated to the presence of human observers at the beginning of the study (from May to mid-October 2004) and the Picnic group was habituated before the second field session (from February to July 2005). The Donga group had three to five adult males, seven adult females, one to two subadult males and one to two infants at a time. The female dominance hierarchy changed between the first and the second field period after the death of the beta female (linearity of the female rank order: MatMan test: first period: $\chi^2_{23} = 48$, $P = 0.002$, $h = 1$, $K = 1$; second and third periods: $\chi^2_{20} = 60.67$, $P < 0.0001$, $h = 1$, $K = 1$). The Picnic group had two to three adult males, four adult females, one juvenile male and two to six infants at a time. The female hierarchy stayed stable throughout the two field periods (linearity of the female rank order: MatMan test: χ^2_{undef} = undefined, $P = 0.373$, $h = 1$, $K = 1$). The genetic relatedness between most members of the groups was known (R. Pansini & R. Noë, unpublished data) and was not correlated with the fact that females were of adjacent ranks or frequent/infrequent grooming partners (C. Fruteau, S. Lemoine, E. Hellard, E. vanDamme & R. Noë, unpublished data).

During the first field period, we followed the Donga group on a regular basis from mid-October to mid-December 2004. Thereafter, we followed each group every second day during the second field period from September 2005 to the end of April 2006 and 2 days in a row every 4 days during the last field period from May 2006 to the end of September 2006. Observations were distributed throughout the day but most data were obtained during 0600 – 1300 and 1400 – 1800

hours. Data were collected by focal group sampling of the adult animals (Altmann 1974), that is, when all adults were visible simultaneously, or by ad libitum sampling when only one observer was in the field or when one adult animal was out of sight or missing from the group. The data represent 605 and 422 h of group focal and 100 and 70 h of ad libitum sampling for the Donga and Picnic groups, respectively. Grooming bouts were timed to the nearest second. A bout was considered to have ended when either the direction of grooming changed or when there was a break of > 20 s.

Data analysis and statistics

For this study, we extracted all grooming sessions in which females interacted. We sorted these sessions into three classes: the sessions occurring between nonmothers and mothers within the 3 months after an infant's birth (Dependant Infant DI period), the sessions occurring between nonmothers and mothers after the 3 months after an infant's birth and the sessions occurring between adult females outside any mating or infant period (hereafter, neutral sessions). Past the 3-month period after their birth, infants were independent enough to interact directly with other members of the group without any interference from their mother (Fruteau et al. 2010). As previous analyses showed that both vervet groups did not show any obvious differences in grooming interactions (C. Fruteau, S. Lemoine, E. Hellard, E. van Damme & R. Noë, unpublished data), we pooled both groups' data to perform the analyses. Tests were performed using R version 2.10.1 (R Core Development Team, Vienna, Austria). The alpha level was set to 0.05.

First, we calculated the occurrence of immediately interchanged grooming during infant handling sessions. We used a *G* test to compare the proportion of reciprocal grooming sessions occurring during and outside the DI period. We excluded from our analysis grooming sessions directly linked to sexual interactions and grooming sessions that occurred during experiments we performed with the vervets (Fruteau et al. 2009). Finally, we used a binomial test to investigate the proportion of grooming sessions initiated by handlers during the DI period and a *G* test to

compare the occurrences of grooming–handling during the DI period with the occurrences during the neutral sessions. In the first case, we considered the null hypothesis to be that mothers would initiate half of the grooming sessions.

Second, to test H_1 we compared the amount of grooming the mothers of the first newborns received during the 15 days prior to the birth with the amount they received during the 15 days after the birth. We also compared, using two-tailed Mann–Whitney *U* tests, the average grooming bout length females gave to mothers and nonmothers during the DI period as well as the average grooming bout length given to mothers during the presence and absence of the infant after the DI period.

Third, to test H_2, H_3 and H_4, we used a linear mixed-effect beyond-optimal model. This model calculates the values of all the fixed effects and their interactions. We used the duration of grooming (s) given by the handlers as the dependent variable. For each grooming point, we used as fixed effects the species (mangabey or vervet), the rank distance between the mother and the handler (this could range from negative to positive numbers), the number of newborn infants (< 3 months of age) per female at this time and the age of the infant (days) when the grooming occurred. We inserted the identity of the handlers as a random effect on the intercept to prevent pseudoreplication. To compare both species we had to log transform the data set. Furthermore, to compare the respective impact of each effect we standardized the data set. To do so, for each data point we subtracted the mean and we divided by the standard deviation.

Finally, to test H_5 and H_6, we used a linear mixed-effect beyond-optimal model. This analysis could only be done on the vervets, as we did not collect the handling times for the mangabeys. We used the duration of infant handling (s) as the dependent variable. Again, we inserted the identity of the handlers as a random effect on the intercept to prevent pseudoreplication. We log transformed the vervet data set so it was normally distributed and we standardized it to compare the impact of each effect. In a first step, for each handling point, we used as fixed effects the duration of the handler's grooming, the rank distance between the mother

and the handler, the number of infants per female at this time, the age of the infant when the grooming occurred and the genetic relatedness between mothers and handlers. We realized that the genetic relatedness did not have a significant effect on handling time. We found a similar result for the rank distance. However, when the rank distance was in interaction with infant's age and number, it indirectly showed that mothers tended to allow longer handling times to some females only. In a second step, and using the fact that previous analyses performed on neutral grooming sessions (C. Fruteau, S. Lemoine, E. Hellard, E. vanDamme & R. Noë, unpublished data) revealed that even if females could choose from six partners in the Donga group and three in the Picnic group, they were mainly interacting with about four and two closely ranked females (hereafter, frequent groomers), respectively. We used the definition cited in Barrett et al. (2000), which considered that groomers were frequent partners if they spent more than 5% of their total active and passive grooming time grooming. Hence, we changed the effect 'rank distance' into the effect 'frequent groomer or not'. To do so, we looked at the identity of both mother and handler and we used a dichotomous variable to characterize the dyad: 'Yes' when the females had been identified as frequent groomers during neutral grooming sessions (C. Fruteau, S. Lemoine, E. Hellard, E. vanDamme & R. Noë, unpublished data), and 'No' otherwise, for all handling times. This change ameliorated the Akaike's information criterion of the model from 819 to 482.

For both linear models and as generalized linear mixed models (GLMM) are robust to an 'almost' normal distribution, we visually assessed the normality of all the residuals using the R function Quantile–Quantile plot (*Q*–*Q* plot).

RESULTS

Infants as a commodity in both mangabeys and vervets

In grooming sessions that involved mothers with small infants there was significantly less reciprocation than in neutral grooming sessions (Table 1): handlers groomed mothers significantly more than vice versa. Furthermore, significantly more grooming sessions were initiated by

handlers (mangabeys: $N = 415$; observed proportion: 1; theoretical proportion: 0.5; $P < 0.0001$; vervets: $N = 142$; observed proportion: 0.96; theoretical proportion: 0.5; $P < 0.0001$).

Groups	**Grooming in infant context (GrInf)**			**Grooming in neutral context (GrGr)**			**G test (df=1) between GrInf and GrGr**
	Reciprocated sessions	Non-reciprocated sessions	% reciprocation	Reciprocated sessions	Non-reciprocated sessions	% reciprocation	
M	75	340	18.1	355	8	97.8	$p = 2.2e^{-16}$ (599.6401)
V	13	129	9.2	292	31	90.4	$p = 2.2e^{-16}$ (307.4824)

Table 1. Grooming patterns in mangabeys (M) and vervets (V)

In mangabeys, 408 of 415 grooming sessions where the mother was holding an infant were immediately followed by infant handling, which is significantly different from the 363 neutral sessions that were not followed by any infant handling (two-tailed G test: $G_1 = 503.225$, $P < 0.001$). We found a similar effect in vervets as 135 of 142 sessions resulted in access to the infant while none of the 323 neutral sessions did ($G_1 = 447.773$, $P < 0.001$). Some infant handling occurred immediately prior to the grooming sessions, but as this represented less than 1% of the total of infant handling in both species, we integrated it with the infant handling occurring after the grooming sessions. In mangabeys, over the 74 cases in which we recorded mothers handling each other's infants, none were preceded or followed by grooming.

Infant market in mangabeys and vervets: multi effects on grooming time

In the 2 weeks after the birth of the first newborn, nonmothers of both species groomed mothers significantly longer than during the 2 weeks before the birth of the infants (two-tailed Mann–Whitney U tests: mangabeys: before birth: average ± SD = 147.39 ± 87.66 s; after birth: 600 ± 64.14 s; $U = 0$, $N_1 = 17$, $N_2 = 28$, $P < 0.001$; vervets: before birth: average ± SD = 145.46 ± 70.40 s; after birth: 342.18 ± 171.56 s; $U = 127.5$, $N_1 = 55$, $N_2 = 46$, $P < 0.001$). Similarly, they groomed mothers for significantly longer than other females during neutral grooming sessions (two-tailed

Mann–Whitney U tests: mangabeys: $U = 6$, N_1=363, N_2=22, $P < 0.001$; vervets: $U = 3313$, N_1=323, N_2= 83, $P < 0.001$; Fig. 1), which confirmed H_1.

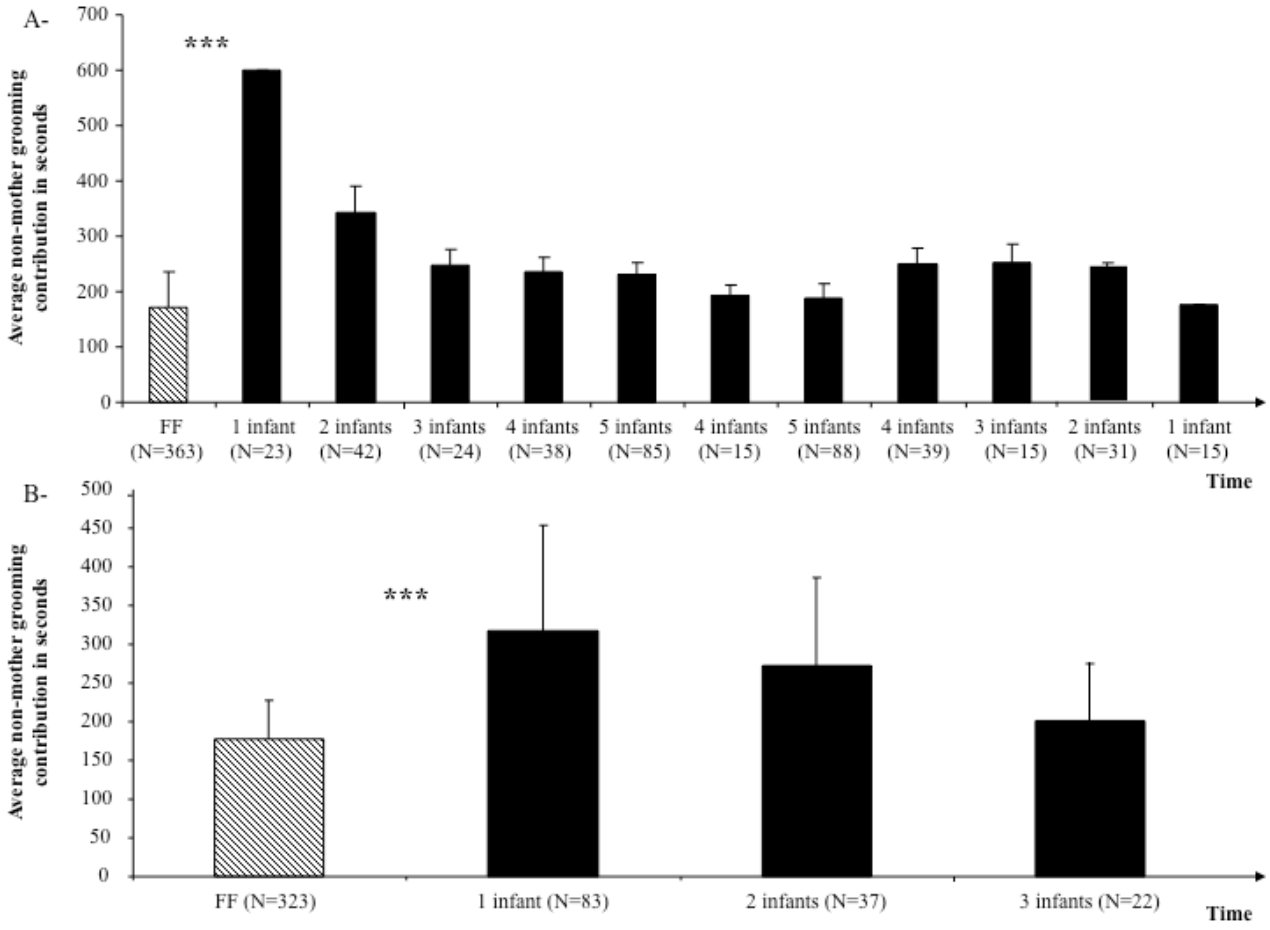


Figure 1. Evolution of non-mothers' grooming investment according to the number of available infants in the group throughout the study period. A- In mangabeys. B- In vervets. Grooming sessions occurring between females during neutral grooming sessions are represented in the FF bars. Grooming sessions occurring between non-mothers and mothers are represented with the black bars. In mangabeys, the number of infants varies quite frequently throughout the study as some of them reached 3 months old before others and one infant also died. This does not happen so much in vervets as the number of infants remains quite low and the lag between two births is short. *** represents $p < 0.001$ (two-tailed Mann-Whitney-U tests to compare the FF investment with the investment handlers gave the mother of the very first new-born). The way grooming investment fluctuate is explained by the GLMM model.

Analyses of the grooming exchanged between nonmothers and mothers after the DI period showed that this effect remained even after infants were starting to be independent: mothers of both species received significantly longer grooming sessions when their infant was clinging on

their fur than when it was not (two-tailed Mann–Whitney U tests: mangabeys: $U = 226.5$, N_1=415, N_2=79 , $P < 0.001$; vervets: $U = 27.5$, $N_1 = 142$, $N_2 = 83$, $P < 0.001$; Fig. 2a).

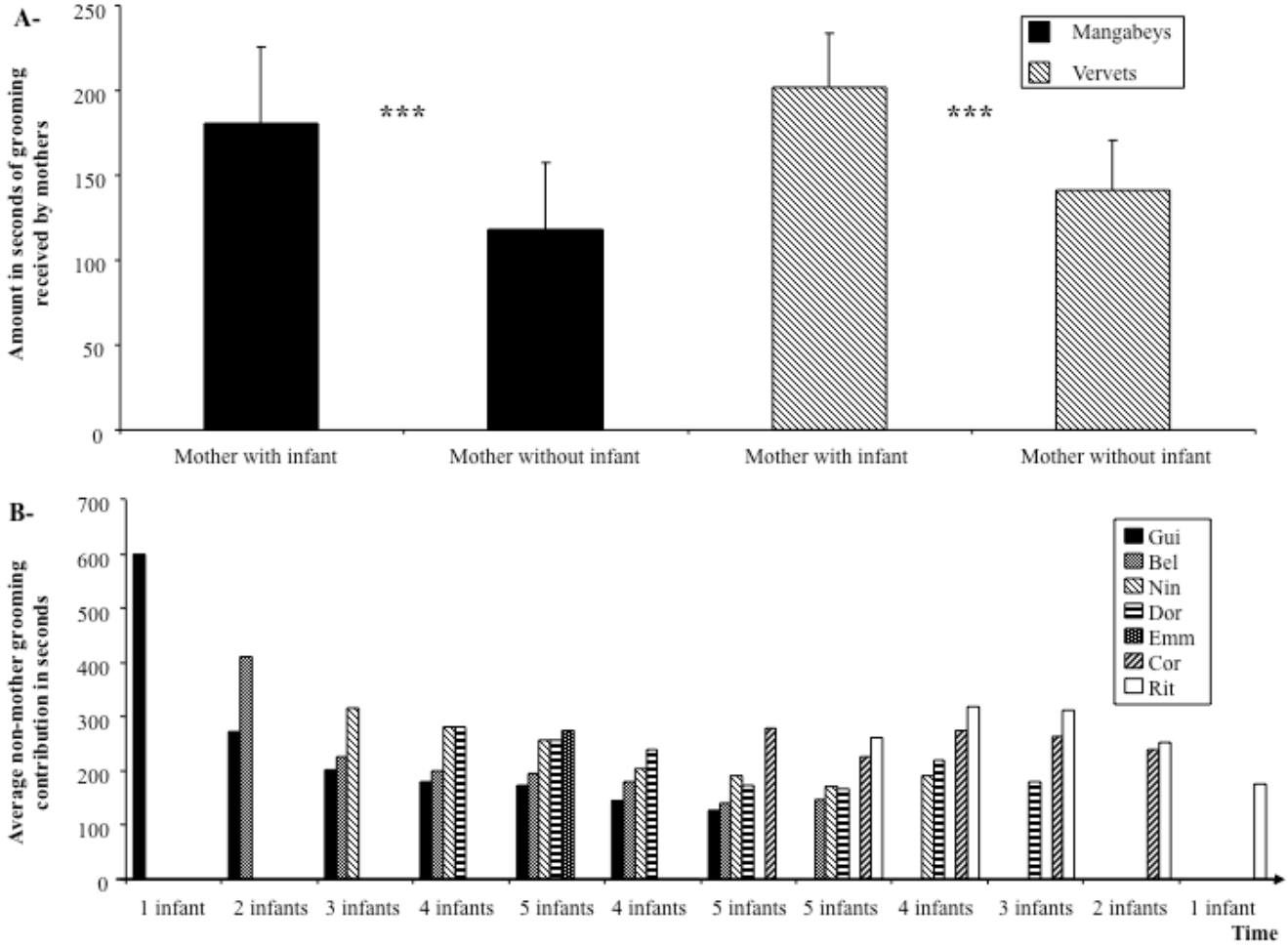


Figure 2. A- Non-mothers' grooming investment toward mothers after the DI period. 'Mother with infants' represents situations when females groomed mothers with suckling infants. *** represents $p < 0.001$ (two-tailed Mann-Whitney-U tests). B- Evolution of non-mothers' grooming investment towards each mother throughout time in mangabeys. In this graph some factors influencing non-mothers' investment (number of available infants as well as the infants' average age) are represented. We did not represented vervets data as we compiled data from two different seasons to run the analysis.

The linear mixed-effect beyond-optimal model (summarized in Table 2) showed significant effects up to the third level of interactions, that is, three effects interacting together. This demonstrates the complexity of the infant market. On the first level of interactions, all four effects (rank distance, number of infants per female, age of infants and species) had a significant impact on the duration of grooming given by handlers. The species effect was the strongest and

showed that vervet handlers groomed mothers significantly less long than mangabey handlers (Table 2). The duration of grooming decreased significantly both when the number of available infants per female in the group increased and when infants grew older (Table 2). Finally, rank distances negatively influenced grooming (Table 2, Fig. 2b). These findings supported hypotheses H_3, H_4 and H_2, respectively.

Effects	Value	Std Error	DF	t-value	p-value
Intercept (Residual: 0.04347578 StdDev: 0.2263636)	5.566336	0.0394879	494	5.479329	**0.0000**
Rank distance	-0.135249	0.0320832	494	-4.215550	**0.0000**
Number infants	-0.605086	0.0371257	494	-16.298293	**0.0000**
Age infants	-0.560262	0.0283301	494	-19.776247	**0.0000**
Species vervet	-3.483899	0.4699516	47	-7.413315	**0.0000**
Rank distance & Number infants	-0.038010	0.0325616	494	-1.167321	0.2428
Rank distance & Age infants	0.051597	0.0246696	494	2.091510	**0.0370**
Number infants & Age infants	0.168124	0.0301330	494	5.579392	**0.0000**
Rank distance & Species vervet	-5.217925	1.1455553	494	-4.554930	**0.0000**
Number infants & Species vervet	-1.527756	0.4635674	494	-3.295651	**0.0011**
Age infants & Species vervet	-2.372648	0.5232095	494	-4.534796	**0.0000**
Rank distance & Number infants & Age infants	-0.043465	0.0250295	494	-1.736558	0.0831
Rank distance & Number.infants & Species vervet	-2.899367	1.0671696	494	-2.716876	**0.0068**
Rank distance & Age.infants & Species vervet	-1.157426	1.2902073	494	-0.897085	0.3701
Number infants & Age infants & Species vervet	-1.377600	0.5551832	494	-2.481343	**0.0134**
Rank distance & Number infants & Age infants & Species vervet	0.164969	1.2768802	494	0.129197	0.8973

Table 2. Summary of the linear mixed-effect beyond optimal model for mangabeys and vervets – the mangabey species is comprised in the intercept and significant effects are double-cycled and in bold.
Fixed effects: log (grooming time) ~ Rank distance * Number infants per female* Age infants * Species | random effect on the intercept: Identity of Handler – AIC: 1059.667

Effects	Value	Std Error	DF	t-value	p-value
Intercept (Residual: 1.164931 StdDev: 0.4557484)	-0.8759489	0.4444397	104	-1.970906	0.0514
Time grooming	0.2956275	0.3672734	104	0.804925	0.4227
Frequent groomers or not	1.0638304	0.5505812	104	2.032195	**0.0461**
Number infants	-1.6566649	0.5377561	104	-3.080700	**0.0026**
Age infants	0.2466319	0.3087754	104	0.798742	0.4263
Time grooming & Frequent groomers or not	-0.1810560	0.4479063	104	-0.404227	0.6869
Time grooming & Number infants	1.5855022	0.4604884	104	0.4604884	**0.0008**
Time grooming & Age infants	-0.3077380	0.1844882	104	-1.668063	0.0983
Number infants & Age infants	0.6506699	0.3700390	104	1.758382	0.0816
Number infants & Frequent groomers or not	2.0150947	0.6484209	104	3.107695	**0.0024**
Age infants & Frequent groomer or not	-0.6112179	0.4360560	104	-1.401696	0.1640
Time grooming & Frequent groomers or not & Number infants	-1.2962133	0.4972428	104	-2.606801	**0.0105**
Time grooming & Frequent groomers or not & Age infants	0.2366608	0.2342527	104	1.010280	0.3147
Time grooming & Number infants & Age infants	-0.2750999	0.2486308	104	-1.106459	0.2711
Frequent groomers or not & Number infants & Age infants	0.4571652	0.4845990	104	0.943389	0.3477
Time grooming & Frequent groomers or not & Number infants & Age infants	0.6402653	0.2847838	104	2.248250	**0.0267**

Table 3. Summary of the linear mixed-effect beyond optimal model for handling in vervets – the infrequent groomers value is comprised in the intercept and significant effects are double-cycled and in bold. Fixed effects: log (Handling time) ~ Grooming time * Frequent groomers or not * Number infants per female * Age infants | random effect on the intercept: Identity of Handler – AIC: 481.9241.

The second level of interactions showed that the rank distance had a stronger influence in vervets than in mangabeys (Table 2) meaning that vervets were more despotic than mangabeys. It also showed that the effects of both infant's age and number per female had a stronger and negative impact on the duration of grooming in vervets (Table 2). Finally, the interaction between

rank distance and infant's age had a significant impact on grooming time (Table 2): when infants were very young, handlers were more closely ranked with the mothers than when infants grew older.

Infant handling in vervets

The linear mixed-effect beyond-optimal model (summarized in Table 3) showed significant effects up to the fourth level of interactions, that is, four effects interacting together. On the first level of interactions the number of infants per female as well as the fact that females were frequent groomers significantly predicted the duration of handling. The duration of handling decreased significantly when the number of available infants increased and when females were not frequent groomers (Table 3). This last finding invalidated H_6.

The second level of interactions showed that grooming times only influenced handling times when they were combined with the number of infants per female (Table 3) meaning that longer grooming bouts only gave longer access to infants when their availability increased. This partially invalidated H_5. It also showed that whatever the number of infants, frequent groomers could handle them for significantly longer than infrequent groomers (Table 3). Except in the fourth level of interactions, the age of infants did not statistically influence handling times.

DISCUSSION

Grooming - Infant exchanges

In both sooty mangabeys and vervet monkeys, grooming patterns of females changed drastically after giving birth. During the 3-month period in which females needed to interact with a mother prior to gaining access to her infant, they essentially initiated grooming sessions and hardly ever received any grooming in return. Rather, in most cases, they were granted access to the infant immediately after grooming its mother. In the weeks following the birth of the first newborn and when still very few infants were available in the group, females groomed mothers for significantly

longer than they groomed other females during neutral grooming sessions. This suggests that they valued handling an infant more than they valued being groomed. As observed by Matsumura (1997) in moor macaques, *Macaca maura*, infants remained attractive even after they became more independent, as nonmothers kept grooming mothers for longer when their infant was suckling than when it was away from the mother.

Analyses revealed that the duration of grooming given by nonmothers was significantly influenced by the infants' availability, their age and the rank distance between the handler and the mother. The number of infants in the group had the strongest effect: when infants were rare, grooming bouts were longer. This suggests that grooming/infant exchanges follow the market law of supply and demand and that the value of infants can vary through time according to their availability. However, supply and demand ratios only partially determined the infants' value. The second major effect was the age of the infant. Nonmothers invested in longer bouts when infants were younger, that is, they groomed a younger infant longer than an older one, everything else being equal. The third effect was the rank distance between handlers and mothers. Basically, to be able to handle infants, higher-ranking females groomed mothers a lot less than did lower-ranking females.

When comparing the grooming durations given by the handlers of both species, we found a very strong species effect on most studied factors. First, for similar rank distances, numbers and ages of infants, mangabey females groomed mothers for significantly longer than vervet females. However, when we compared the lengths of grooming bouts females gave to be groomed in return, we found similar durations for both species (mangabeys: 171.5 ± 64.5 s; vervets: 161.5 ± 162.5 s; C. Fruteau, S. Lemoine, E. Hellard, E. vanDamme & R. Noë, unpublished data). Hence, this significant species effect may point at more competition among nonmothers to obtain access to infants. In fact, the number of infants per female is bigger in vervets than in mangabeys and as soon as more than two infants are born in the group, vervet females groom mothers as long as they

would groom any other female. This finding is not surprising as vervet groups are rather small: few infants are needed to reach the 'infant/handler' carrying capacity of the group.

In the light of our results, we can assume that in mangabeys and vervets, the length of grooming gives an accurate price for each available infant, as its range of variation seems large enough to reflect many small changes. Indeed, the market value of infants depends on multiple factors (relationships of dominance, outbidding competition, supply and demand ratios, etc.) and fluctuates with time. The market almost changes from one interaction to the next and females need to adjust their grooming behaviours constantly, which they seem to accomplish accurately too. The mechanisms that lead to these quick and accurate adaptations deserve further study.

Infant handling

Recent studies (Henzi & Barrett 2002; Schaffner & Aureli 2005; Gumert 2007a; Slater et al. 2007) have considered infants as exchangeable commodities whose value can be assessed thanks to grooming or embraces by nonmothers, but little has been said about the other side of the market: the quality of the infant handling obtained by the groomer. 'Infant handling' is a tricky parameter, however, that can be described on either a quantitative level (duration or rate of handling) or a qualitative level (intensities of interaction such as 'smell the infant', 'touch it', 'groom it', 'carry it'). In this paper we only investigated the quantitative effects in terms of handling duration for a small number of adult females in vervets and further studies would be needed to refine our results. A first result showed that handling time increased when infants were rare or when females and mothers were frequent grooming partners. Whatever the number of infants, frequent groomers could handle them for significantly longer than infrequent groomers. Contrary to expectations based on contingent reciprocity models, grooming and handling times were not directly correlated. Longer grooming bouts did not necessarily secure longer handling, especially when infants were rare. Grooming durations were correlated with handling time only when infant ratios were above one infant per female.

Without additional information, our findings on infant handling could provide evidence for all four hypotheses concerning females' attraction to newborns. However, even though females sometimes pulled infants' arms or legs, they handled them with care and low-ranking mothers could easily retrieve their infants from higher-ranked females in both species, which contradicts the reproductive competition hypothesis (Hrdy 1976). Similarly, females who had had infants in previous years were as interested in handling infants as nulliparous ones were, which invalidates the allomothering hypothesis (Lancaster 1971; see also Fairbanks 1990). Furthermore, handling times were not directly affected by infants' maturity, which seems to contradict the by-product hypothesis (Silk 1999). Thus, our results seem to follow the alliance formation hypothesis that Manson (1999) suggested in the light of his results on capuchins, *Cebus capucinus*, in which mothers of infants less than 3 months old allowed longer handling times to females they had frequently interacted with prior to giving birth.

So far, handling time has been the only investigated reward parameter and may not be the best measure to illustrate what is at stake when females handle infants. It would be interesting to have results on the qualitative aspects of the handling: maybe longer grooming would allow females to carry or groom infants even for a short while, while shorter grooming would only allow them to touch or smell an infant. However, from a situation in which females competed to gain access to young infants, grooming bouts seemed to secure cooperation from the mother. Indeed, although mothers did not easily give access to their infants, they tolerated handling as soon as they received the necessary amount of grooming, which showed how market rules could influence grooming/infant trades.

ACKNOWLEDGEMENTS

We thank the Ministère de la Recherche Scientifique, the Ministère de l'Agriculture et des Ressources Animales, the CSRS, the CRE and the Taï Monkey Project in Ivory Coast and the Mpumalanga Parks Board, UNISA and ABEERU colleagues, L. Brown, L. Barrett, S. P. Henzi

and R. Bshary in South Africa for research permission and logistic support. We thank G. Gha, R. Peho and F. Range in Ivory Coast and S. Aubel, A. Barrett, A. Brotz, D. Carter, V. Dufour, E. Hellard, S. Lemoine in South Africa for assistance in the field. We thank N. Poulin for statistical advice and two anonymous referees whose advice greatly improved the manuscript. Max-Planck-Institut für Verhaltensphysiologie, CNRS and NWO (Evolution and Behaviour 051-12-036) provided financial support.

CHAPTER 4

Infanticide risk and infant defence in multi-male free-ranging sooty mangabeys (*Cercocebus atys*)

Part I: Sexual Selection in mangabeys

Cécile Fruteau, Friederike Range, Ronald Noë

2010. Infanticide risk and infant defence in multi-male free-ranging Sooty Mangabeys, Cercocebus atys. Behavioural Processes, 83, 113-118.

F Range

ABSTRACT

For years, infanticide by males was thought to be unlikely in multi-male primate species. Recent studies have, however, presented evidence of infanticide in such species and a recent model by Broom and colleagues predicts that males' age and rank influence the occurrence of infanticide: youngest and highest ranking immigrant males are more likely to commit infanticide than their older and lower ranking counterparts if putative fathers fail to protect infants. I collected data on adult free-ranging sooty mangabey females in the Taï National Park, Ivory Coast, over eleven months including a birth and a mating season. Infanticide had been previously reported in captivity for this species, but not in the wild. Several males entered the group prior to and during the mating season. As predicted by the model, only the more dominant immigrant ones attacked mother-infant pairs significantly more often than did other males. Mothers often reacted with counter-attacks. Potential fathers guarded and supported infants and mothers throughout the period of infant vulnerability. Furthermore, as only one of seven infants died despite 136 observed attacks on mother-infant pairs and unattended infants by immigrant males, we conclude that cooperation between putative fathers and mothers represents an effective protection against infanticide.

Deliberate killing of infants by adult males has been reported for many mammal species and is frequent in primates (e.g. Hrdy 1974, Angst & Thommen 1977, Janson & van Schaik 2000, van Schaik 2000). No less than five explanations have been proposed, including, among others, the social pathology hypothesis (Dolhinov 1977, Boggess 1984) that predicts infanticide in primates living in unnatural environments and the by-product hypothesis (e.g. Sussman et al. 1995) in which infanticide is a side effect of males' general aggression. The most widely accepted explanation for infanticide in non-human primates however, is the sexually selected infanticide hypothesis (Hrdy 1974, 1979, Hrdy & Hausfater 1984). It states that an adult male may increase his fitness by killing unrelated and unweaned infants if he can easily mate with the mother afterwards: the female victim of infanticide immediately resumes her sexual cycle and after having defeated the former resident male, the infanticidal male gain an earlier opportunity for siring the next offspring (e.g. Borries et al. 1999a, Pussey & Packer 1994, contributions in van Schaik & Janson 2000). Hence, in its original formulation, this adaptive scenario was restricting infanticide to non-seasonal breeders characterised by a single-male mating system. However, many studies reported infant killing by males in both multi-male (e.g. Collins et al. 1984, Borries et al. 1999a, Soltis et al. 2000, Weingrill 2000) and seasonal breeders (e.g. Wright 1995, Borries 1997) and this new range of infanticide occurrences led to new predictions about the way males may gain reproductive benefits. In multi-male breeders, newcomer males are then expected to use infanticide if they reach a status in the male hierarchy that allows them to mate with females (Broom et al. 2004). In seasonal breeders, males are expected to commit infanticide quite early after the infant's birth so that females can resume ovulation either before the end of the mating season or right at the very beginning of the next one (see Wright 1995).

In species in which males tend to commit infanticide, females are expected to develop counter-strategies to minimize the risk of infant loss (Hrdy 1979; Smuts & Smuts 1993). A first strategy involves behavioural changes during the period after birth when infants are vulnerable to infanticide. This can include avoiding unfamiliar males or constraining infants in their presence

(e.g. Collins et al. 1984, Fairbanks & Mc Guire 1987, Hauser 1988, Sommer 1994, Wright 1995), counter-attacking infanticidal males (e.g. Mohnot 1971, Hrdy 1977), and finding allies such as related females or potential fathers to help them protect infants (e.g. Smuts & Smuts 1993, Treves 1998, 2000, Borries et al. 1999b, Palombit et al. 2000). A second strategy involves behavioural and physiological changes prior to conception. Since most male primates are thought to be unable to recognise their offspring as such (e.g. König 1989, but see Alberts 1999, Buchan et al. 2003), they probably restrain their aggressive behaviours towards infants of females they mated with (Noë & Sluijter 1990, van Schaik & Kappeler 1997). Thus, females can mate promiscuously in order to induce paternity confusion (Hrdy 1979, Hrdy & Whitten 1987, Nunn 1999, van Schaik et al. 1999) or display sexual swellings at times it is unlikely for them to be ovulating (Gordon et al. 1991, Zinner & Deschner 2000). In this paper we only focus on the first option, i.e. behavioural changes during infant vulnerability.

Mangabeys (*Cercocebus spp.*) are both promiscuous and seasonal breeders and infanticide occurrences have been reported in both captive sooty mangabeys (*C. torquatus atys*, Busse & Gordon 1983, Gust et al. 1995) and free ranging crested mangabeys (*C. galeritus galeritus*, Gust 1994). Preliminary observations of several non-resident males attacking mothers and infants in our study group gave us reason to suspect infanticide to occur in wild sooty mangabeys (*C. torquatus atys*) as well. In our group the average inter-birth interval was 29 ± 7 months (N = 28 females) and females who lost their infants during the six-months period after birth immediately resumed menstrual cycles while females whose infants remained alive or lived longer than six months did not. Thus, non-resident males could gain an earlier opportunity to mate with mothers (at least a whole year) by committing infanticide at an early stage after infants' births. We therefore investigated the potential risks for infanticide and their likely consequences. We first hypothesised that if infanticide may occur, it would essentially be performed by non-resident males. Hence, we expected (1) these males to mainly target mothers and infants rather than other members of the group. More precisely and as suggested by the recent model from Broom and

colleagues (2004), we expected (2) these aggressive males to be young and to sufficiently integrate the group to quickly rise in the male hierarchy. Secondly we hypothesised that if infanticide risks were real, some adult members of the group would develop counter-strategies. More particularly, we expected (3) potential fathers to actively protect mothers and infants and (4) females to seek the proximity of these males. Eventually and still following the model by Broom and colleagues (2004), we expected (5) these protector males to be older and dominant resident males.

METHODS

Research areas and subjects

This study was conducted in the Taï National Park in south-western Ivory Coast (6°20'N to 5°10'N and 4°20'W to 6°50'W). The park is the last remaining major block of West Africa primary forest. It covers approximately 454,000 ha. With a mean annual rainfall of 1875 mm, a mean annual temperature of 24°C (Taï Monkey Project data, 1991-1999) and a distinct dry season from December to March, the forest is classified as "tropical moist forest" (Whitmore 1990). At least twelve primate species, including sooty mangabeys (*Cercocebus atys*), live in the park.

The group was well habituated to human observers prior to the start of this study and was followed from dawn to dusk by at least one observer during the entire study period from November 2001 to August 2002. During this period, 7-14 adult males, 35 adult females, about 70 sub-adults and juveniles were observed in the group. Seven infants were born between December 10, 2001 and March 10, 2002. Seven of the adult males ("residents") were present in the group over the entire study period. Altogether, seven other adult males ("non-residents") joined the group for various periods of time during this period. Five of those ("immigrants" males) entered the group in February, stayed until the end of the study and integrated the male hierarchy. The two other non-resident males remained in the group for very short periods (from a couple of hours to a couple of days at a time). We therefore focused the analyses on the five immigrant males only.

On average, mangabeys (*Cercocebus spp.*) have a gestation period of about six months (Deputte 1991) and a lactation that can vary between four/five months (wild *Cercocebus albigena johnstonii*: Rowell & Chalmers 1970) and six/ten months (*C. galeritus* in Groves 1978). In our study species (*C. torquatus atys*) the lactation period seemed to last longer (from 12 up to 18 months). However, this difference may result from the fact that no accurate terminology defines when a lactation period really ends. In our group, the six surviving infants of the year started to eat diverse food around five/six months but were still suckling regularly. At least 21 juveniles born the previous years were still regularly suckling at the beginning of the study: 13 of them stopped when they were about 12 months old and the rest carried on to regularly suckle and cling on mothers till after they were 18 months old. The birth season was comprised between December and March with a peak around February (Range & Noë 2002). The mating season usually started in May and lasted up to the end of September with a mating activity peak in July-August.

Data collection

The analyses presented in this paper are based on conflicts and proximity data recorded during focal animal and *ad libitum* sampling (Altmann 1974). Conflicts were recorded when one individual threatened, darted at and potentially chased over few meters, pushed on the ground or bit another individual. Proximity was considered when two individuals were less than 5 meters apart.

We conducted 15-min focal samples on adult females with at least 60 minutes between consecutive samples of the same individual and three minutes between samples of different individuals. However, for the analyses we also used the focal samples that were at least nine minutes long (89 samples over 2272) if they were truncated because of the observer loosing the subject after an obstacle. For each focal animal, we recorded each minute on the minute (instantaneous sampling, Altmann 1974): the infant's presence / absence and distance and the nearest adult female and male within 5 meters. Social interactions were recorded continuously

(detailed ethogram in Range & Noë 2002). Due to limited visibility in the early evening, we opted for an opportunistic sampling schedule conducting focal samples only between 7 a.m. and 4 p.m.

Between November 1, 2001 and August 20, 2002 we collected 1360 hours worth of *ad libitum* data and a total of 568 hours of focal samples for all of the 35 adult females (ranging from 63 to 65 per female).

Data Analysis and statistics

Each time we performed analyses between categories of individuals, we corrected for their respective numbers: resident males: N = 7, immigrant males: N = 5, mothers: N = 7, non-mothers: N = 28, juveniles between one and two years old: N = 21 and unattended infants: N = 6.

Dominance

We compiled two socio-matrices (one for adult males, one for adult females) in which we used the recorded approach/retreat and threat/retreat unidirectional interactions to determine the subordinate individual of each dyad. For both males and females, the rank-order among adults was strictly linear (Matman with 10000 randomisations: Kendall's coefficient of linearity: K = 0.967 for both gender, $\chi^2 = 48$, $p = 0.0017$, df = 25.12 for males, $\chi^2 = 447.89$, $p < 0.0001$, df = 40.86 for females).

Infants' vulnerable period to infanticide

As females whose infants died within the six months after birth were observed to resume menstrual cycles, we assumed these six months to be a good estimate of the period during which males would benefit more from infanticide. Hence, we defined these six months as the period during which infants may be vulnerable to infanticide (vulnerable period VP hereafter).

During the vulnerable period, infants grew more and more independent and could be left unattended for short periods of time. We defined infants as being unattended when they were at

more than three meters from their mothers for more than one minute. One infant died while he was still continuously clinging on his mother so we removed him from analyses performed on unattended infants.

Statistics

Non-parametric statistical tests (Siegel & Castellan 1988) were conducted using Statview (version 5.0.1). Analyses of conflicts and male-female proximities were conducted using Chi-square (χ^2), Mann-Whitney-U tests and Spearman correlations. Results were considered as being significant when $p \leq 0.05$. If multiple n tests were conducted on the same data set, we set the total experiment wise error rate α at 0.05 and the corrected α' were taken from Narum reference table with critical values for the Bonferroni correction method (2006).

RESULTS

Pattern of aggression of adult males towards females and infants

We summarized the males' attacks in Table 1.

	Mothers	Non-mothers	Infants	Juveniles	NR-M	R-M
NR-M	92	25	36	2	9	11
R-M	8	29	0	4	138	21

Table 1: Attacks of males to other classes of individuals. NR-M: non-resident males; R-M: resident males.

In order to test the hypothesis of infanticidal risk, we analysed the pattern of aggression of adult males toward adult females, juveniles and unattended infants. During the study, we observed 154 conflicts between adult males and adult females, 117 of which were conducted by immigrant males (attacks against mothers: $N = 92$, attacks against non-mothers: $N = 25$) and 37 by resident

males (mothers: N = 8, non-mothers: N = 29). Immigrant males were significantly more aggressive towards mothers than towards non-mothers (two-tailed Chi-square test $\chi^2 = 81.408$, $p < 0.001$, df = 10). Resident males, in contrast, attacked mothers at similar rates than they attacked non-mothers (two-tailed Chi-square test $\chi^2 = 0.084$, $p = 0.999$, df = 1) (Fig. 1). On average, over the whole 1360 hours we spent observing the study group, an immigrant male would be likely to attack a female with infant 2.63 times while he would only attack a female without infant 0.18 times.

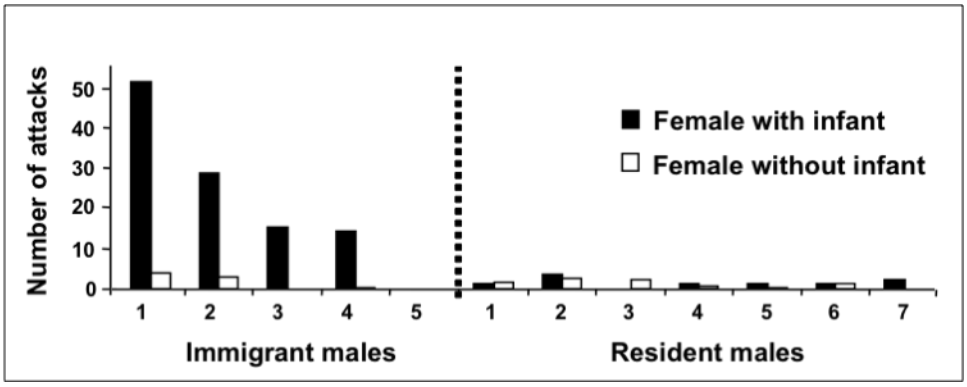


Figure 1: Number of attacks performed by immigrant and resident males towards females with and without infants. Males of each category are ordered by rank. 1 represents the highest-ranking male of the category.

The attacks from both male categories were very distinct. Attacks from immigrant males started as soon as they entered the study group. Usually they would dart at mothers, coming quickly on their back and would grab their fur or a part of their infant's body, push them on the ground and quickly try to bite. Females would loudly scream and look around for support. In contrast, resident males mainly tended to slap females during the reproductive season. Usually a female at the beginning of her menstrual cycle would start to present her sexual parts to males. Old resident males would inspect them once or twice before turning around. Then the female would leave. However, some would insist and present again and again leading the male to threaten and slap them.

Immigrant males conducted 36 attacks against unattended infants and only 2 against juveniles between one and two years of age. In contrast resident males never attacked unattended infants and attacked juveniles four times. Immigrant males significantly targeted unattended infants more than juveniles of less than two years (two-tailed Chi-square test $\chi^2 = 42.318$, $p < 0.0001$, $df = 1$). Due to the small sample size for resident males, we did not perform any statistical analysis.

Among the immigrant males, we found a negative correlation between the rate of aggressive behaviours and their respective rank-order in the group (spearman correlation: $r = -1$, $p = 0.0455$). As suggested by Broom and colleagues (2004), higher-ranking immigrant males were more aggressive toward mothers and infants than their lower-ranking counterparts. Furthermore, we also found a positive correlation between the number of mounts they could perform and their respective rank-order (spearman correlation: $r = 0.98$, $p = 0.0456$). In fact, two of the immigrant males reached the male alpha position during the mating season. During their tenure, they could form consort and mate with receptive females without being displaced by other adult males.

Unfortunately, as immigrant males were coming from non-habituated groups, we could only have a rough estimation of their age. Hence, we did not try to correlate their age with their level of aggression.

Pattern of aggression among adult males

In order to test the hypothesis of infant protection by resident males, we analysed conflicts among adult males. We observed 178 conflicts among the five immigrant and seven resident adult males. Immigrant males attacked another adult male (resident or immigrant) 20 times while resident males attacked 158 times. A resident male was significantly more likely than an immigrant male to attack another adult male (two-tailed Chi-square test $\chi^2 = 38.398$, $p < 0.0001$, $df = 1$). Among these resident males, two males showed significantly higher rates of aggression towards other

males (150 attacks; two-tailed Chi-square test $\chi^2 = 90.455$, $p < 0.0001$, $df = 1$ and Chi-square test $\chi^2 = 15.828$, $p < 0.0001$, $df = 1$) (Fig. 2). Of these 150 attacks, 129 (86%) were directed towards immigrant males after they had first attacked mother/infant pairs or unattended infants (Fig. 3).

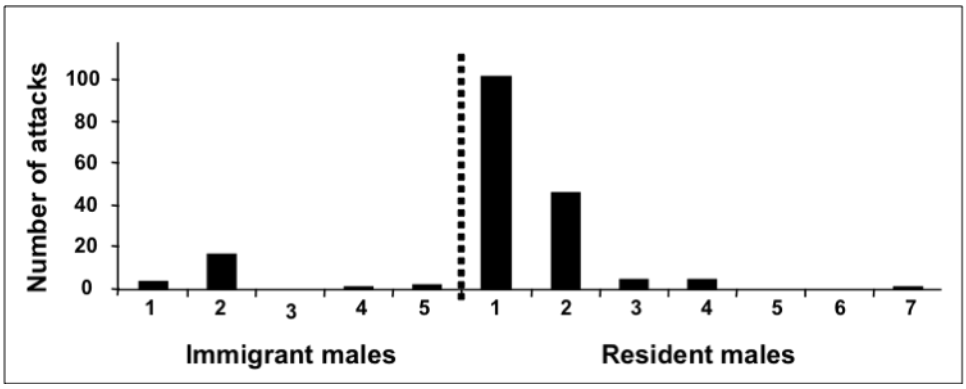


Figure 2: Number of attacks performed by immigrant and resident males towards another male (either immigrant or resident). Males of each category are ordered by rank. 1 represents the highest-ranking male of the category.

To summarize: immigrant males attacked mother/infant pairs and unattended infants 128 times. The two resident males protected females and infants by themselves on 116 occasions and simultaneously on 13 occasions. We henceforth categorised them as "protective" (PR) males. The protection could vary from a simple threat (opened mouth with visible teeth) with a slight forward movement of the body to chases, slaps and bites. The threat mainly happened when females had counter-attacked with other females (five times) or when infants were already more than three months old and clinging on their mothers (47 times). Chases and slaps occurred when a PR male darted at an immigrant male: when this male remained close to the females or infants (20 times), the PR male slapped him on the face and shoulders; when he jumped and fled (44 times), the PR male chased him over long distances (> 50 meters) for few minutes. Eventually, the PR males' simultaneous actions were the most intense. One PR male would first dart at the immigrant male and the second PR male would follow few seconds afterwards. The three males would end up rolling on the ground with many grunt vocalisations and biting each other. All 13 actions occurred after immigrant males tried to grab and bite unattended infants.

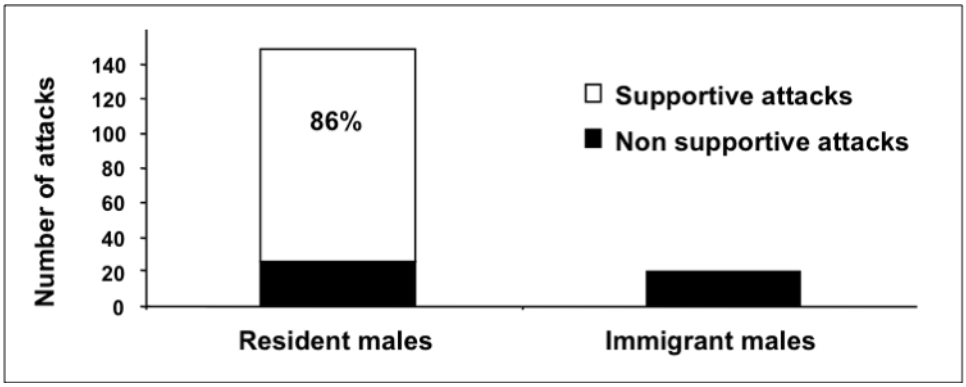


Figure 3: Number of attacks performed by immigrant and resident males towards another male (either immigrant or resident). In white is represented the proportion (86%) of attacks given in support of aggressed mothers while in black is represented the proportion of attacks that were not performed in support of aggressed mothers.

It is to note that outside the infant context, males hardly fought each other. Indeed we recorded only 49 fights and all occurred during the mating season. One immigrant male performed 9 of these fights in order to gain access to the alpha female that was precociously receptive, hence, reaching the alpha position on the 07/02/02. His tenure lasted until the 30/07/02 when a second immigrant male challenged him in four fights and won the access to the only female that was receptive this week.

Among the resident males, we found that the two PR males were the highest-ranking males, which corroborates the predictions by Broom and colleagues (2004). In the general male hierarchy, they were second and third higher-ranking males. Based on previous observations of the group we assume that they were also among the three oldest males of the group. Furthermore, during the previous mating season these two males were seen to form consortships and mate with the seven mothers when they were receptive (Benetton et al. *master manuscript*).

Aggression by females

During our study, we observed 392 agonistic interactions of females towards other adult members of the group. The following tests (N = 4) required a Bonferroni correction with $\alpha' = 0.01250$.

Adult females attacked other adult females 283 times and adult males 109 times, a difference that is not statistically significant when taking the number of females and males into account (34 females, 12 males; two-tailed Chi-square test $\chi^2 = 0.318$, $p = 0.5730$, $df = 1$). The 28 females without infants directed attacks significantly more often at adult females than at adult males (225 attacks against females and 25 against males; two-tailed Chi-square test $\chi^2 = 21.680$, $p < 0.0001$, $df = 1$). However, 5 of the 25 attacks against adult males were in support of attacked mothers. Furthermore, females without infants directed aggression less often against mothers than against other adult females (23 attacks against mothers and 202 against females corrected for number of mothers and non-mothers; two-tailed Chi-square test $\chi^2 = 9.180$, $p < 0.0023$, $df = 1$). The seven mothers were significantly more aggressive against adult males than against adult females (58 attacks against females and 84 against males; two-tailed Chi-square test $\chi^2 = 31.808$, $p < 0.0001$, $df = 1$). Almost all of the attacks of mothers directed against adult males (82 out of 84) were counter-attacks in response to one of the 128 attacks by an immigrant male, i.e. the mothers counter-attacked in 64% of cases (Fig. 4).

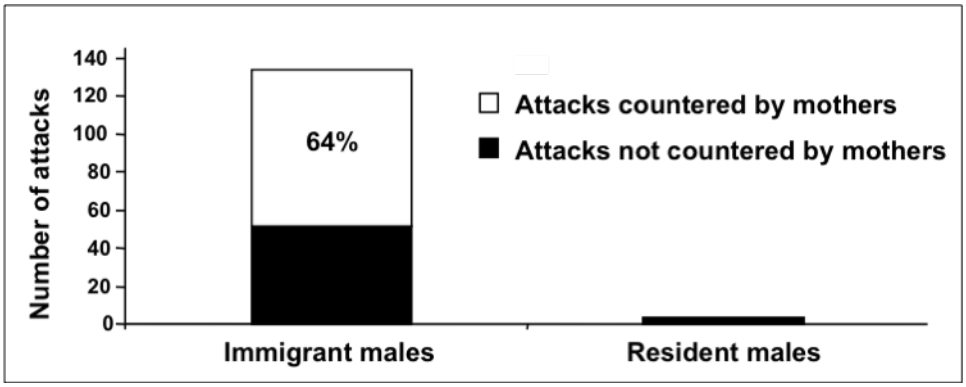


Figure 4: Number of attacks performed by immigrant and resident males towards mothers or unattended infants. In white is represented the proportion (64%) of attacks countered by mothers while in black is represented the proportion of attacks that were not countered by mothers.

Each time immigrant male's attacks aimed unattended infant, mothers would roughly grab their infant and turn around the male to try to bite him. In other cases, females would try to slap the male or would even chase him along with the PR male.

Proximity between males and females

In order to test the hypothesis of bonding between mothers and putative fathers as a counter-strategy for infanticidal risk, we analyzed the pattern of proximity between mothers and adult males. The following tests (N = 4) were corrected by Bonferroni with $\alpha' = 0.01250$. Per 100 minutes of observation, mothers were close to resident males 72.35 minutes (ranging from 65 to 79 minutes) during the vulnerable period (VP) of their infants, and 33 minutes (ranging from 24 and 54 minutes) when their infants were more than six months old (not vulnerable period NVP).

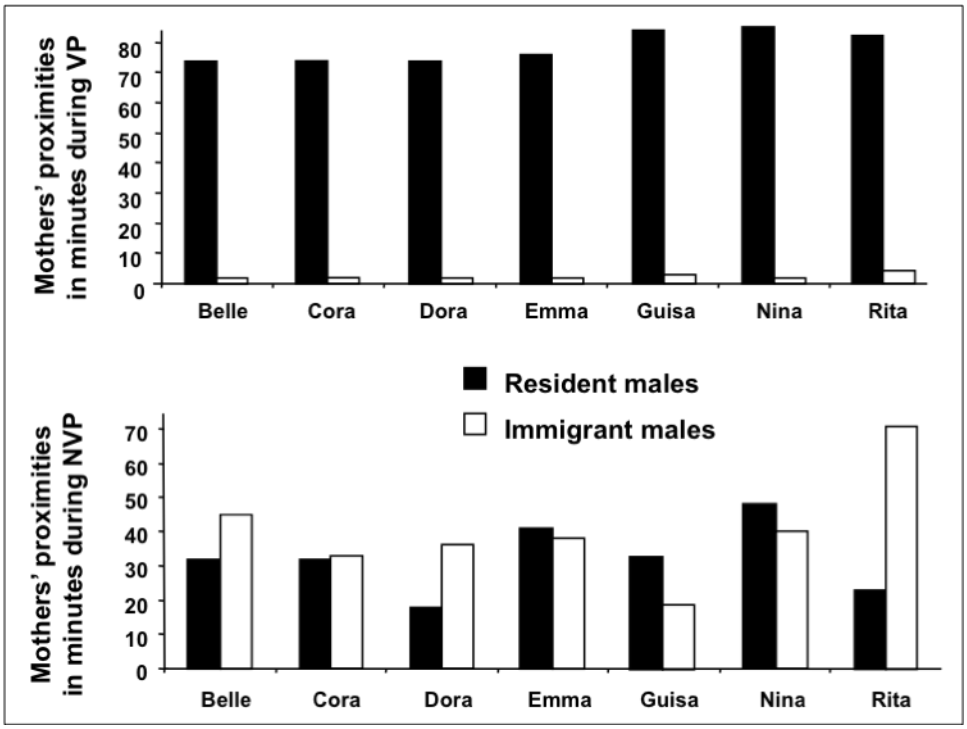


Figure 5: Number of minutes per 100 minutes of observation during which mothers were observed at close proximity (less than 5 meters) from resident and immigrant males. The first graph represents the proximities during the six months after infants were born and were considered particularly vulnerable to infanticide (VP). The second graph represents the proximities after infants were more than six months old (NVP).

Hence, mothers were significantly closer to the resident males during VP than during NVP (two-tailed Mann-Whitney-U test: U = 0.00, p = 0.0017). In contrast, mothers were close to immigrant males only 8 minutes (ranging from 5.35 and 12.5 minutes) during the vulnerable period of their infants, and 33 minutes (ranging from 18 and 47 minutes) when their infants were more than six

months old, which shows that mothers were closer to immigrant males during NVP than during VP.

Hence, if mothers were recorded at a comparable distance to resident and immigrant males when their infants were more than six months old (two-tailed Mann-Whitney-U test: $U = 15.5$, $p = 0.2502$), they were significantly more often registered near resident males than near immigrant males during VP (two-tailed Mann-Whitney-U test: $U = 49$, $p = 0.0017$) (Fig. 5). Furthermore, PR males were observed to actively gather mothers and infants after attacks by immigrant males.

DISCUSSION

Infanticidal risks in mangabeys: aggression by-product or behavioural strategy under sexual selection?

In the by-product hypothesis, infanticide is not a selected behaviour. Infants are not injured or killed intentionally but because they are the most vulnerable individuals of the group. Hence, infants' killing could happen during any males' intense enough conflicts. In this case, infants would have the same probability to be injured by resident or immigrant males and males would not target mothers and infants more than any other member of the group. Rather, infants' injuries would happen when males are fighting each other and mothers either interfere in the conflict or remain close-by. Furthermore, as the killing behaviour is accidental, females would not develop any particular behavioural counter-strategies to prevent it. Conversely, in the sexually selected hypothesis, infanticide is a behavioural strategy and concerns males that did not mate with mothers the previous year. More precisely, the model developed by Broom and colleagues (2004) predicts the occurrence of infanticide in multi-male primate species, if (1) male attackers' costs are negligible and/or if (2) their status in the group allows them to get almost exclusive access to the receptive females. Under this hypothesis, only some males would benefit from infanticide and would target mothers and infants more than other member of the group. Furthermore, as infanticide would be a selected behaviour, females would develop some counter-strategies.

In our study group, males did not fight each other very often and conflicts always arose when the access for a receptive female was at stake. These conflicts did not last over long periods and mainly involved the two protagonist males. Indeed, we recorded only four coalitions and neither mothers nor females without infants were seen to intervene. Furthermore, no juveniles or infants were involved in these conflicts, either intentionally or accidentally. In contrast, and mainly outside the mating season, some of the immigrant males seized every opportunity to attack mother/infant pairs or unweaned and unattended infants without any provocation from the females (*pers. obs*.). None of these males had been seen mating with any of the group's females the previous year (Benetton et al. *in prep*.). These same males hardly ever targeted juveniles or females without infants. Resident males, in contrast, were more likely to attack females without infants than mothers of dependent infants. Hence, the pattern of conflicts performed by the males in our group tends to validate the sexually selected hypothesis rather than the by-product one.

Resident males' frequent counter-attacks probably made the infanticidal costs particularly high for immigrant male attackers. Beside the risks of getting injured, the intensive chases they had to flee from were likely to be energetically costly. However, if the costs were not negligible, at times, the menstrual cycles of up to four females were synchronised. It allowed up to four high-ranking males to form consortships simultaneously. As predicted by the sexually selected hypothesis, most of the immigrating male attackers rose in the male hierarchy quickly after they entered the group. Two of them even reached the alpha position during the course of the study and increased their chances of siring the females' next offspring, as male ranks and mounting success tend to be correlated.

During our study, one infant died before reaching one month old. A few days before the infant's death, the mother was seen with a large and infected wound on her leg. At the same time, the infant held its head on a strange angle and showed a general weakening which started with an abnormal lethargy (indifference to surrounding group members). As we did not witness how the mother and her infant were injured, we cannot give any evidence that this was the consequence of

a direct attack by a male. However, the mother had been attacked regularly before her infant died (8 attacks in 12 days) but was rarely attacked thereafter (4 attacks in the remaining 179 days). She displayed a large sexual swelling within a month after the loss of her infant while mothers with surviving infants did not. During the mating period, she was also seen mating with the two immigrant male attackers that reached the alpha position. In this respect immigrant males that rose in the male hierarchy were able to gain sexual access to a receptive mother and our results are in agreement with many other studies supporting the sexual selection-hypothesis of infanticide.

Mothers' counter-strategies: counter-attacks and cooperation with potential fathers

As expected with the sexually selected hypothesis, mothers developed strategies that seemed to reduce infanticidal risks. First, they regularly counter-attacked immigrant male attackers during the infant's vulnerable period despite a sexual dimorphism that largely favours males during aggression. Indeed males are larger, heavier and have longer canines and mangabey females, as many other primate females (Hrdy 1977, Palombit 1999), seem to fail to form effective coalitions against males. We recorded only five occurrences during which some females helped mothers. However, if these mutual supports were rare, they involved at least from two to six other females and did not seem correlated to matrilineal affiliations. Counter-attacks by females can probably only partially reduce the risk of infanticide.

Resident adult males, however, that mated with the female and therefore were potential sires, can provide considerable support for a mother against a potential infanticidal male (Hrdy 1979). Resident males who had been observed mating with the females the previous year (Benetton et al. *in prep*.), strongly supported both infant/mother pairs and stray infants, and were sometimes seen to groom the aggressed mothers after they had been attacked by immigrant males (24.3% of the cases). These protective males were among the oldest and the highest-ranking males of the group. Furthermore, mothers were recorded in close proximity of at least one resident male during the period of infant vulnerability, while they avoided immigrant males. Our findings

therefore corroborate the results of some other studies on infanticide (e.g. Palombit et al. 1997, Borries et al. 1999b, Palombit 1999, 2000, Janson 2000), the mother/resident male cooperation is therefore likely to be the key to reducing infanticide risk in sooty mangabeys.

Conclusions

Infanticide in mangabeys really follows model's predictions step-by-step. Firstly, male attackers were usually immigrant males. They had no history of mating with the mothers of unweaned infant they targeted and they managed to reach a position in the male hierarchy that allowed them to have privileged accesses to receptive females. Secondly, protective males were resident and old males. The previous mating season, they were seen to mate with the mothers of unweaned infants. Thirdly, after the birth of their infants and to reduce infanticidal risks, mothers used behavioural counter-strategies such as staying in the close vicinity of protective males. Eventually, it would be interesting to investigate whether mangabey females also developed counter-strategies prior to the conception of the infants.

ACKOWLEDGEMENTS

We thank the Ministère de la Recherche Scientifique, the Ministère de l'Agriculture et des Ressources Animales, the CSRS, the CRE and the Taï Monkey Project in Ivory Coast for research permission and logistic support. We thank G. Gha, R. Peho and F. Range in Ivory Coast for assistance in the field. Max-Planck-Institut fuer Verhaltensphysiologie, CNRS and NWO (Evolution and Behaviour 051-12-036) provided financial support.

CHAPTER 5

Mating market in sooty mangabeys (*Cercocebus atys*): females' grooming behaviours vary according to the operational sex ratio

Part II: Sexual Market in mangabeys

Cécile Fruteau, Nicolas poulin, Eric van Damme, Ronald Noë

In revision Behavioral Ecology

C & JM Fruteau

ABSTRACT

Sooty mangabeys have a clear mating season during which males are expected to compete over receptive females, both by fighting over access to females as well as by gaining favours of females through affiliative behaviours. In this study, we investigated the relations between grooming sessions and sexual activities in a group of sooty mangabeys from the Taï forest, Ivory Coast. We compared the length of grooming bouts adult males and females exchanged with each other according to the receptive state of the female. In contrast to most species, we found that females were the active gender seeking for sexual opportunities while males only concentrated their sexual effort towards females displaying maximal tumescence. Most of grooming sessions were not reciprocated by males but directly followed or preceded by mating. Females tended to groom low-ranking males before they mate, while high-ranking males were groomed after the mount. Furthermore, females gave longer grooming bouts to males when they were receptive than when they were not. However while they were receptive, the length of the bouts decreased when they were close to ovulation (stage 4 sexual swelling) and when more males were available in the group. These findings demonstrate that grooming-sex exchanges in mangabeys follow biological market predictions as supply and demand as well as partners' intrinsic value influence the grooming durations. Hence in mangabeys, females compete for access to certain males, probably because resident males function as a protective shield against infanticidal males and because multi-male mating is thought to deter infanticide through paternity confusion.

In primates with multi-male - multi-female groups and clear reproductive seasons, the operational sex ratio (OSR; Emlen & Oring 1977) is almost always skewed in favour of the females. This implies that male reproductive success is likely to be limited by the access to receptive females and that there will thus be heavy competition among males over access to such females. This can either take the form of contest competition whereby females passively accept the winner of the competition, or a competition for the favours of females, with females playing a more active role by choosing their preferred partners. However, some males may use one or more forms of sexual coercion, such as mate guarding, forced copulation and infanticide (Niemeyer & Anderson 1983, Smuts & Smuts 1993, Clutton-Brock & Parker 1995, van Schaik & Janson 2000). This, in turn, may make the access to certain males that can offer protection an important source of competition among females. Some authors (Rubenstein 1986; Wrangham & Rubenstein 1986; Wrangham 1987) formulated the "hired gun" hypothesis in which they predicted that some males would indirectly enhance their chance of mating by choosing to actively defend resources during intergroup encounters: receptive females would preferentially mate with males that defend resources (Fashing 2001). Other authors (Palombit 1999, 2000; Palombit et al. 2001) demonstrated that male - female bonding considerably reduced infanticidal risk in some species: potential fathers helped mothers to protect infants against aggressive males (see also Fruteau et al. 2010).

Hence, sexual relationships can be seen as a form of cooperative exchange between two individuals driven by conflicting interests. Under this scope, biological market theory (Noë & Hammerstein 1994, 1995) may be an interesting framework to investigate how economic rules can influence both social and sexual interactions occurring among and between trader classes. Males would constitute one trader class and females would form the other class. The dynamic of exchanges between the two classes would follow basic market laws such as: a) partner choice depends on expectations of better profits an individual can get with a partner rather than with another and b) the supply and demand market law determines the values of the exchanged

commodities (Noë 2001). Furthermore, competition over access to the rare partners would be expected among the members of the more common trading class and would increase the value of the exchanged commodity (Noë 2001).

Recent studies produced contradictory results on how well biological market may explain exchanges in primates (e.g. Barrett et al. 1999; Henzi & Barrett 2002; Payne et al. 2003; Schino et al. 2003; Manson et al. 2004; Gumert 2007a; Schino et al. 2007; Gumert & Ho 2008; Frank & Silk 2009; Fruteau et al. 2009; Tiddi et al. 2010). However, many of them demonstrated that grooming could be traded against grooming (e.g. Barrett et al. 1999; Manson et al. 2004) or against other commodities, such as access to infants (e.g. Henzi & Barrett 2002; Fruteau et al. resubmitted), access to appetent food (e.g. Ventura et al. 2006; Fruteau et al. 2009) and even tolerance (e.g. Barrett et al. 1999; Payne et al. 2003; Gumert & Ho 2008). Barrett & Henzi (2001) predicted that grooming could also be exchanged against compliance of mates. They expected that males would be the ideal gender to exchange grooming with mating as sexual selection theory emphasizes on males' aptitude to develop costly traits and/or skills to attract mates. More specifically, they argued that males could use grooming to bond with a female thereby enhancing their chances to mate with her afterwards. Following this lead, Gumert investigated the factors influencing sexual relationships in long-tailed macaques (2007b) and was the first to produce direct evidence that grooming could be exchanged against mating (see also for indirect evidences: e.g. Hemelrijk et al. 1992; Colmenares et al. 2002). He expected long-tailed macaques to be an ideal species to test market predictions on male's grooming investments, as males seemed to usually initiate sexual relationships while females seemed to mainly select the appropriate partner. He found that males indeed groomed females in order to secure sexual relationships and that proximate economic factors such as the supply of receptive females or the value of a partner, affected males' grooming investments.

As for longtailed macaques, sooty mangabey (*Cercocebus atys*) females present exaggerated anoperineal sexual swellings. In many species, females' receptivity is not accurately

predicted by their swellings. However, in species with exaggerated swelling such as mangabeys, the maximum perineal tumescence (stage 4) usually corresponds with the periovulatory phase of their sexual cycle (Whitten & Russell 1996, Nunn 1999). Hence, the different stages of swelling constitute a convenient graded signal to estimate the period when females are sexually receptive and to accurately estimate the number of receptive females in the group at any time. Even though mangabeys have a clear reproductive season, in the year we performed this study, only up to six females over 28 could be synchronously receptive. At times, up to 12 adult males and 18 adolescent males were present in the group. This set up makes male competition a strong possibility. It should allow to investigate whether males use grooming as a commodity to secure a mating and consequently to investigate whether market rules influence males grooming investments. However, in this species, if females remain in their natal group, males emigrate. Numerous non-resident males enter groups prior to and during the mating season and are usually aggressively targeting mother/young infant pairs. As a consequence, mangabey females use several anti-infanticidal strategies. Mothers of young infants notably gather around resident males, who are also the putative fathers of the infants, and benefit from their active protection during conflicts engaged by the non-resident males (Fruteau et al. 2010). However, the females actually start their anti-infanticide efforts during the mating season prior to infant birth by engaging in multi-male mating in order to confuse paternity (Wolff & Macdonald 2004). Therefore, and contrary to classical sexual selection predictions, the sexual market may concern females rather than males and investigation on females' grooming investments toward specific males should not be neglected.

In this study we thus observed the grooming and sexual behaviours of both adult males and females. Similarly to Gumert (2007b), we first determined how much of male-to-female grooming and of female-to male grooming were directly related to sexual activities such as inspection of the sexual parts and/or mounts. In a second step if such grooming sessions could be observed, we tested whether they were really traded for sexual opportunities. More specifically we

predicted the following.

Male competition

We expected that if grooming sessions were traded for sex, males would mainly groom receptive females and invest in longer bouts when the grooming is directly associated with sexual activities. We expected that the value of each partner would influence the grooming durations: as high-ranking males usually get better access to females (e.g. Collishaw & Dunbar 1991; de Ruiter & van Hoof 1993) they should invest in shorter bouts than their lower-ranking counterparts. Similarly, high-ranking females and females displaying maximum tumescence should benefit from the market and be groomed longer than lower-ranked females or females displaying the first swelling stages. Furthermore, as in all grooming markets, we expect the OSR to influence the exchange rate. We predict that males grooming investment toward females would be negatively influenced by the value of the OSR, i.e. numerous males would have to groom receptive females longer in order to mate and males would groom longer when few receptive females are available.

Female competition

If female competition intervenes in the sexual market, we predict that females would initiate grooming sessions with males more often when they display sexual swellings that when they do not. Furthermore, when receptive females groom males, males should increase their chance to mate. Similarly to male competition, females grooming investments should be influenced by each partner's value as well as the OSR. Finally, as females' competition over male access may reflect an anti-infanticidal strategy, we could expect that they bias their grooming efforts toward immigrant males or low-ranking males in order to multiply the mating and confuse paternity (graded-signal hypothesis, Nunn 1999; Wolff & Macdonald 2004).

METHODS

Research areas and subjects

We conducted this study in the Taï National Park in south-western Ivory Coast (6°20'N to 5°10'N and 4°20'W to 6°50'W) between November 1, 2001 and August 20, 2002. The park is one of the last remaining major block of West Africa primary forest and covers approximately 454,000 ha. The forest is classified as "tropical moist forest" (Whitmore 1990) with a mean annual rainfall of 1875 mm, a mean annual temperature of 24°C (Taï Monkey Project data, 1991-1999) and a distinct dry season from December to March. At least twelve primate species, including sooty mangabeys, *Cercocebus atys*, live within its boundaries. The study group's home range covered an area of about 7 km^2, near the western border of the park.

Our study group was well habituated to human observers prior to the start of the study and was followed from dawn to dusk by at least one observer during the entire study period. The group was not provisioned and we recognised all adult, subadult and infant members by facial features. During the study we observed 7-14 adult males, 35 adult females, about 70 juveniles and sub-adults. Seven infants were born between December 10, 2001 and March 10, 2002. One died on February 2, 2002. Seven of the adult males ("residents") were present in the group over the entire study period. Altogether, seven other adult males ("non-residents") joined the group for various periods of time during this period. Five of those ("immigrants" males) entered the group in February, stayed until the end of the study and integrated the male hierarchy. The two other non-resident males remained in the group for very short periods (from a couple of hours to a couple of days at a time).

Adult females display exaggerated sexual swellings when entering receptive cycles. Exaggerated swellings start at stage 1 with a light pinkish oedema around the clitoris area, reach their peaks at stage 4 (about one week later and for two to three days) with a huge and bright red oedema covering the entire anoperineal area and then start to decrease to disappear after three to

two days. The complete swelling cycle lasts about two weeks. Even if females' receptivity is not accurately predicted by their swellings, the maximum perineal tumescence (stage 4) corresponds with the periovulatory phase of their sexual cycle (Whitten & Russell 1996, Nunn 1999; Wolff & Macdonald 2004).

Data collection

We focused the data collection on adult females. We used the "approach/retreat" and "threat/retreat" unidirectional interactions to determine the female dominance hierarchy. It remained stable throughout the study period (linearity of the female rank order: MatMan test: $\chi^2_{41} = 447.89$, $p < 0.0001$, $h = 0.97$, $K = 0.97$). We used both *ad libitum* and focal sampling observation techniques (Altmann 1974) to collect data on grooming sessions occurring between males and females. When grooming sessions occurred between males and receptive females, we recorded whether the grooming interaction was directly preceded or followed with sexual activities such as the inspection of sexual parts or mounts. We use the term "grooming session" for an uninterrupted interaction between two individuals. Each session can consist of one or more "grooming bouts", i.e. a period over which a single individual grooms another without interruption. The length of grooming bouts was rounded to the 30 nearest seconds. A new bout was assigned when the direction of grooming changed and a new session when there was a ≥ 30 seconds break between bouts. We used 15-min focal sampling with at least 60 min between consecutive samples of the same individual and 3 min between samples of different individuals. However, for the analyses we also used the focal samples that were at least 9-min long (89 samples over 2272) if they were truncated because of the observer loosing the subject after an obstacle. For each focal animal, we recorded each minute on the minute (instantaneous sampling, Altmann 1974): the infant's presence / absence and distance and the nearest adult female and male within 5 meters. Social interactions were recorded continuously (detailed ethogram in Range & Noë 2002). Due to limited visibility in the early evening, we opted for a sampling schedule from

7:00 to 16:00. We collected a total of 568 hours of focal samples for all of the 35 adult females (ranging from 63 to 65 per female). All females were followed at least once every three days and we randomized each female's sampling to account for the time of day. *Ad libitum* data were recorded all day long (even while doing focal sampling on a subject) as soon as a social interaction (aggression, grooming, mount, etc.) occurring between two identified individuals was observed. Sexual swellings stages, births, immigrations, disappearances and encounters were recorded on a daily basis.

Data analysis and statistics

During the study period, 29 out of 35 adult females displayed at least one incomplete swelling cycle (they did not reach either the stage 4 or the stages 3 and 4). We extracted all grooming sessions in which adult males and females interacted and we sorted these sessions according to the receptivity stage of the female and the fact that grooming was directly linked to a sexual activity. We also extracted all the sexual activities occurring between adult partners. Tests were performed using R (version 2.10.1). The alpha-level was set 0.05.

In a first step, we investigate how adult males and females interacted when females were receptive. We used binomial tests to compare the proportion of sexual activities initiated by males and females and to compare the proportion of each activity (inspection of sexual parts and mounts). We assumed that either gender would have the same probability to seek sexual favours and that partners would engage in both sexual activities with the same probability. We used G tests to compare the rate of grooming initiation performed by each gender when females were receptive and when they were not. During the reproductive period, we also used a G test to investigate the occurrence of grooming - sexual activity interactions when females were receptive or not. We considered that grooming and sex were directly associated when less than one minute separated both events. As we recorded many such associations in which grooming could happen prior to or after the mount, we investigated whether the identity of the male or more precisely, its

rank in the hierarchy, could explain the sequence of events by using a logistic regression following a binomial law.

To test the effects of both females' receptivity and of the OSR on females' grooming investment, we used a linear mixed-effect beyond optimal model. We used the duration of grooming (in seconds) given by the females as the dependant variable. For each grooming point, we used as fixed effects: the swelling stage of the female (ranging from 1 to 4) and the OSR value. For the OSR, we counted from 1 to 6 receptive females and from 10 to 12 males at times. We inserted the identity of the females as a random effect on the intercept to prevent pseudoreplication. Furthermore, we log-transformed the grooming durations so the model's residuals were normally distributed, and in order to compare the respective impact of each effect, we standardised the data set.

RESULTS

Sexual activities and grooming patterns

	Swelling stage 0	Swelling stages 1-3	Swelling stage 4
Female initiated	0	376	86
Male initiated	0	125	234
Total	0	501	320

Table 1. Sexual activities initiation according to the receptive stages of the adult females.

During our study we recorded 821 sexual activities occurring between adult males and females (Table 1; Fig.1). When females were not fully receptive (stages 1 to 3), they initiated sexual activities significantly more often than males (Nfemales = 376, Nmales = 125, observed proportion for females: 0.75, theoretical proportion: 0.5, $p < 0{,}001$) and the activities mainly consisted in the presentation of their sexual parts so that males could inspect them (Ninspections = 327, Nmounts = 174, observed proportion for inspections: 0.65, theoretical proportion: 0.5, $p < 0{,}001$). However, when females presented maximum tumescence, males initiated sexual activities

more often than females (Nfemales = 86, Nmales = 234, observed proportion for males: 0.73, theoretical proportion: 0.5, $p < 0{,}001$) and the activities mainly switched from inspection to mounts (Ninspections = 21, Nmounts = 299, observed proportion for mounts: 0.93, theoretical proportion: 0.5, $p < 0{,}001$).

Pair	Initiator Female	Initiator Male	Total	Reciprocation
RecF-ResM	110	17	124	4
RecF-ImM	49	6	55	5
NonRecF-ResM	33	3	36	32
NonRecF-ImM	25	38	63	47

Table 2. Number of grooming interactions initiated by both adult males and females during the mating period. RecF = receptive female; NonRec = non receptive female; ResM = resident male; ImM = Immigrant male.

During the mating season, we recorded 281 grooming sessions between adult males and females: 99 sessions occurred between males and non-receptive females and 182, between males and receptive females (Table 2). When females were receptive, grooming sessions with immigrant males were mainly initiated by females (49 of 55 sessions). This significantly changed from when they were not receptive as they initiated only 25 of 63 sessions ($G = 7.134$, $df = 1$, $p = 0.0075$). Conversely, for resident males no such effect of the females' receptivity was apparent: when females were receptive they initiated 110 of 127 sessions and when they were not receptive, they initiated 33 of 36 sessions. Hence the proportion of grooming sessions initiated by females was comparable ($G = 0.043$, $df = 1$, $p = 0.836$).

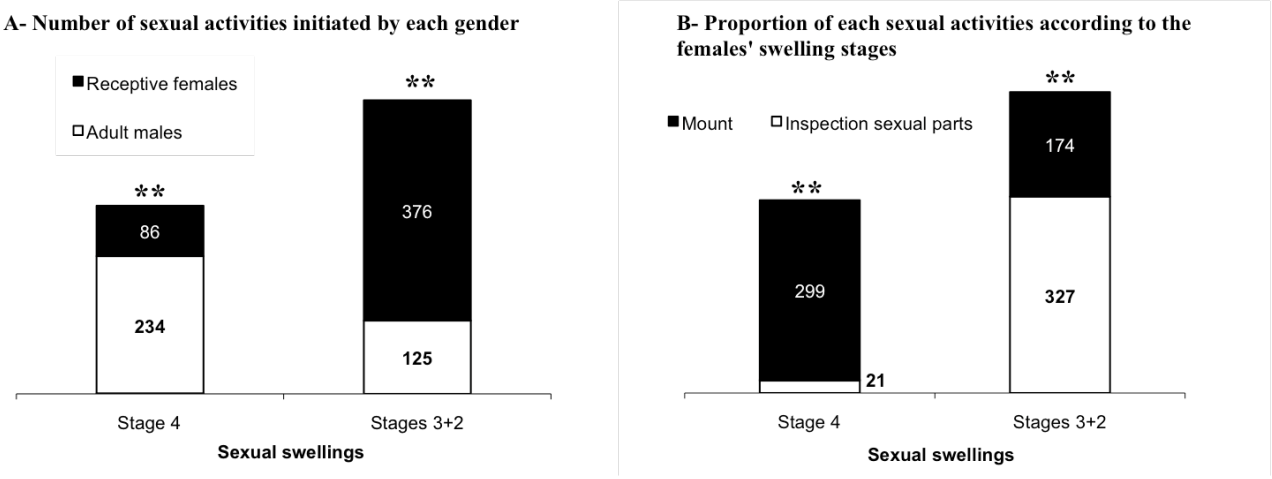


Figure 1. A- Number of sexual activities initiated by each gender. B- Proportion of each sexual activities according to the females' receptivity. ** represents a $p < 0.001$ (binomial tests).

Females' receptivity also affected grooming reciprocity within a session. Immigrant males groomed back females significantly more often when they were not receptive (47 of 63 sessions) than when they were receptive (5 of 55 sessions) ($G = 24.783$, $df = 1$, $p < 0.001$). We found similar effect with resident males: they reciprocated grooming more often when females were not receptive (32 of 36 sessions) than when they were receptive (4 of 127) ($G = 58.339$, $df = 1$, $p < 0.001$) (Fig. 2A).

Furthermore, the probability that a grooming session and a sexual activity were associated was $P = 231/821 = 0.28$. Only one of the 99 sessions with non-receptive females was followed by a sexual activity while theoretically such association should have occurred 27.9 times. With receptive females, 172 of the 182 sessions were either preceded or followed by a sexual activity, which contrasted with the 51.2 theoretical occurrences. Hence, grooming with receptive females secured significantly more sexual opportunities than grooming with non-receptive females ($G = 68.407$, $df = 1$, $p < 0.001$).

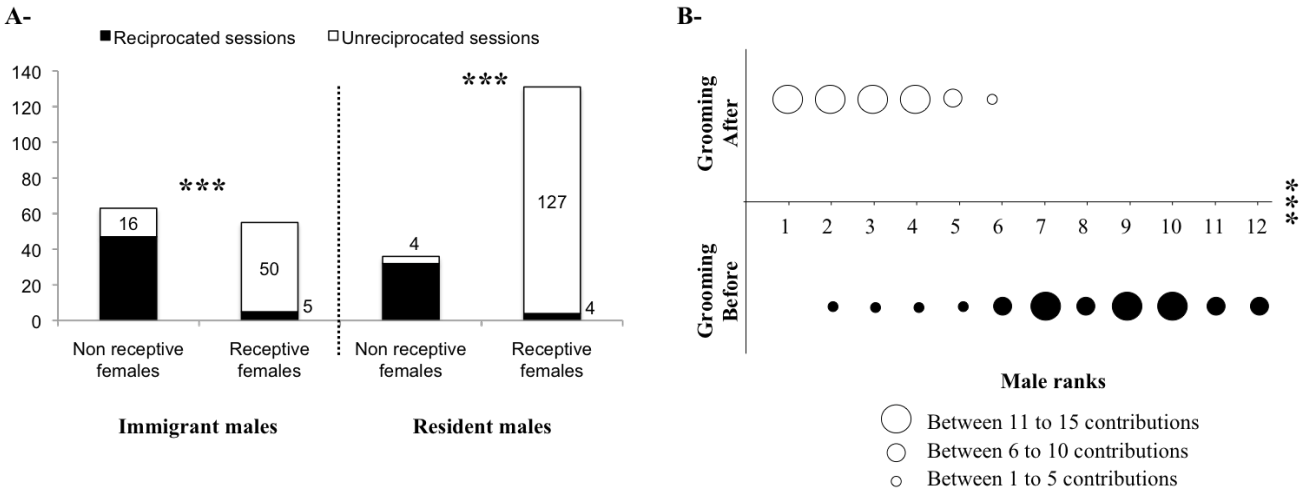


Figure 2. A- Amount of grooming sessions reciprocated or not by males. Data were separated between immigrant and resident males and consist on the amount of grooming sessions that males reciprocated or not when females were receptive or when they were not receptive (G tests). B- Influence of male ranks on the period females groomed them in exchange for mating. White circles represent the proportion of grooming sessions taking place after the mating while black circles represent grooming sessions occurring prior to the mating. Circle sizes represent each male contribution for both cases of grooming. *** represents a $p < 0.0001$ (logistic regression).

Finally, for all males combined, 97 grooming sessions occurred directly before the sexual activity and 75 took place directly after. Females groomed higher-ranking males significantly more often after the mating while they groomed lower-ranking males significantly more often before (logistic regression: $z = 5.561$, $p < 0.0001$) (Fig. 2B).

Grooming, sexual swelling and male availability

During the mating period, of the 182 grooming sessions occurring between adult males and receptive females, we observed 36 sessions taking place with females displaying a stage 4 swelling, 54 sessions with females in stage 3 swelling, 50 sessions with females in stage 2 swelling and 42 sessions with females in stage 1 swelling. When receptive females displayed a stage 1 or a stage 2 swelling, they groomed males significantly longer than when they were not receptive (respectively: $U = 1066.000$, $p < 0.001$ and $U = 1974.000$, $p = 0.042$). Conversely, when they displayed a stage 4 swelling, they groomed males significantly less than when they were not

receptive (U = 1374.000, p = 0.040). When they displayed stage 3 swellings, they groomed males about equally often than when they were not receptive (Mann Whitney U test: U = 2594.000, p = 0.760) (Fig.3).

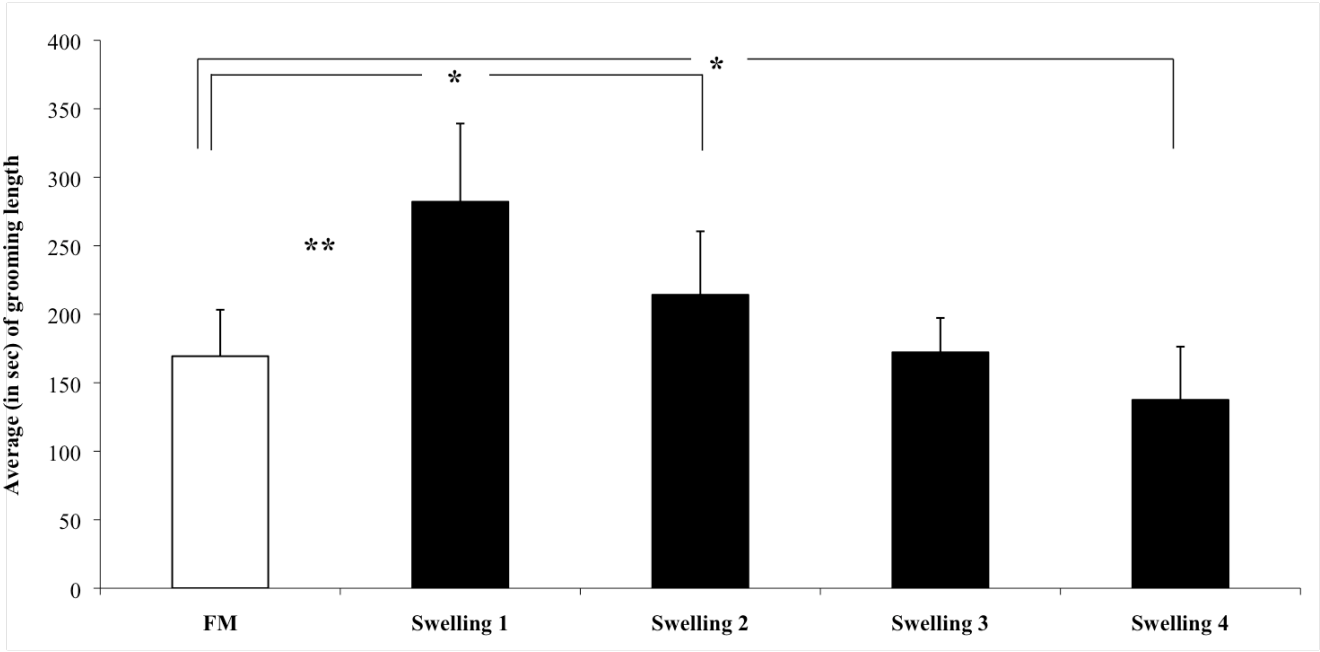


Figure 3. Comparison of average grooming bout lengths females invested into males during the reproductive period. We compared their investment when they were receptive or not and according to their swelling stages. Average lengths are given in seconds. Swelling stages are from 4 to 1, 4 being the swelling climax surrounding ovulation and 1 the very first and very last steps of the sexual cycle. ** represents a $p < 0.001$ and * represents a $p < 0.05$ (Mann Whitney U tests).

Effects	Value	Std Error	DF	t-value	p-value
Intercept (Residual: 0.3979922 StdDev: 0.08006741)	0.0123985	0.03559655	143	0.348306	0.7281
Swelling stage	**-0.5541470**	**0.03161071**	**143**	**-17.530355**	**0.0000**
OSR	**0.7844312**	**0.03110411**	**143**	**25.219534**	**0.0000**
Swelling stage & OSR	**-0.1314553**	**0.03190534**	**143**	**-4.120165**	**0.0001**

Table 1. Summary of the linear mixed-effect beyond optimal model – significant effects are double-cycled and in bold.

Fixed effects: log (grooming time) ~ Swelling stage * OSR | random effect on the intercept: Identity of Female – AIC: 205.233

From one to six receptive females and from 10 to 12 males were observed simultaneously in the group at any time. The grooming contributions of receptive females were highly influenced by both their swelling stage and the OSR (beyond optimal linear model: AIC; Table 1). Females groomed males significantly longer when they were in a stage 1 swelling than when they had a swelling of higher stage (value = -0.507, $p < 0.0001$). They also groomed significantly longer when the OSR was higher, i.e. when less males were available (value = 0.778, $p < 0.0001$). The combined effect of swelling and OSR revealed that when females displayed stage 4 swellings, their grooming investments were less impacted by the OSR (value = 0.082, $p = 0.0076$) (Fig.4).

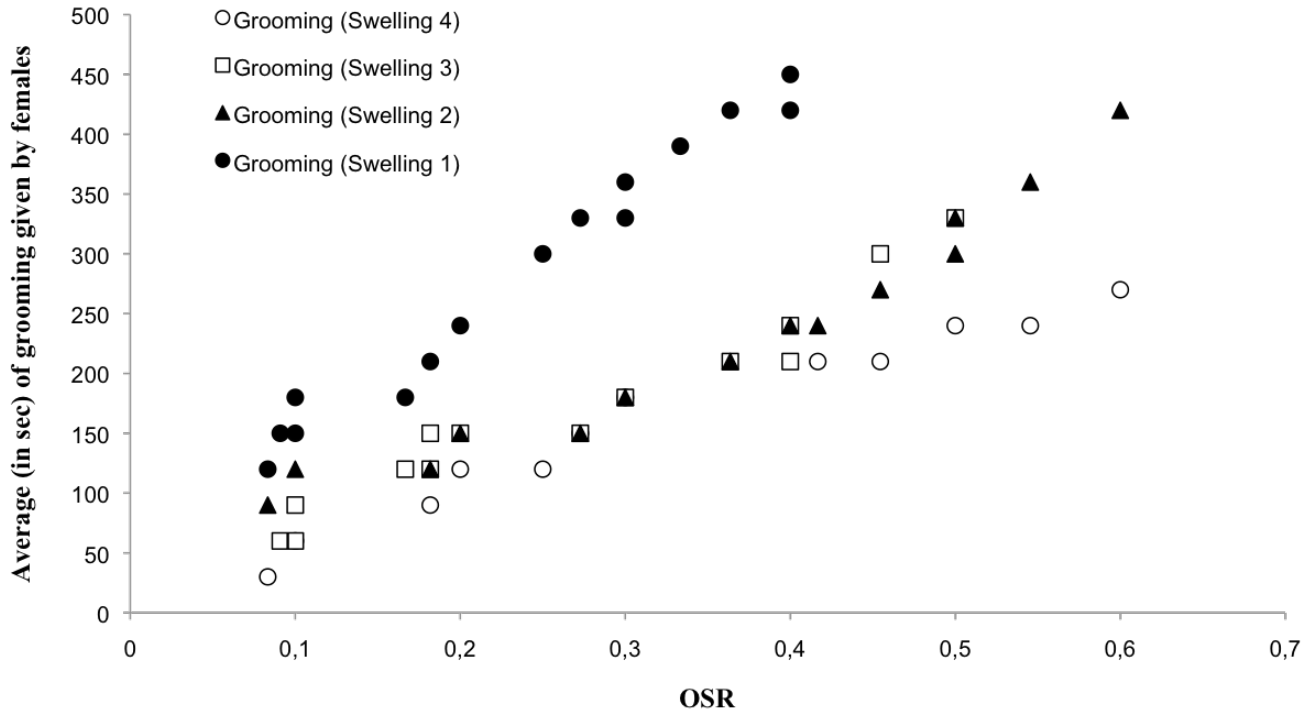


Figure 4. Average in seconds of grooming length receptive females invested into males in exchange for mating and according to the OSR. Each OSR depends on the number of adult males (from 10 to 12) and on the number of receptive females (from 1 to 6) at times in the group. Each average grooming value is given according to the swelling stage the female was displaying.

DISCUSSION

Females' interest in seeking for sexual opportunities

In sooty mangabeys, males and females sexual roles were not as classical as in other primate species such as longtailed macaques. For instance, adult males were eager to initiate sexual relationships and consortships only when females presented maximum swellings. Then the sexual activities mainly consisted in mounts. When they were not fully receptive (stages 1 to 3), and in stark contrast with macaque females, mangabey females seemed to be the active gender seeking for sexual opportunities: they repeatedly presented their sexual parts to males so that males could inspect them, often masturbated after a male refusal to mate and produced loud copulation calls that attracted surrounding males (unpublished data). Furthermore females seemed to use grooming sessions as a strategy to promote some mating. First, they were shown to act differently toward immigrant males than toward resident males in term of grooming initiation. Indeed with resident males, they initiated grooming sessions about as often when they were receptive than when they were not. With immigrant males, they initiated the sessions more often when they were receptive. Second, males, both residents and immigrants, were shown to hardly reciprocate grooming sessions when females were receptive, which contrasted with the classical grooming pattern we recorded when females were not displaying sexual swellings. In such case, males would also groom females. Third, receptive females' grooming secured sexual activities prior to or after the grooming session while non-receptive females' grooming did not lead to any sexual opportunity.

The difference in how females reacted to resident and immigrant males may be explained by the different nature of their relationships. In a previous study, females and resident males were shown to actively cooperate to reduce infanticidal risks (Fruteau et al. 2010). Hence, females may use grooming to keep the bond with certain males intact. In the case of non-resident males however, females may initiate grooming sessions when they are receptive in exchange for multi-male mating (MMM: Wolff & Macdonald 2004). Multi-male mating is thought to enhance paternity confusion and thereby deters infanticide risks. When females are not receptive however,

immigrant males may try to form bonds with females in order to be accepted in the group. In this case, they are the gender looking for the social contact.

The MMM hypothesis may also explain for the moment receptive females chose to groom males: they groomed higher-ranked males more often after the mount but groomed lower-ranked males more often prior to the mating. Mangabey females give loud copulation calls directly after the mount, which attracts other males (unpublished data). We observed that when females were displaying very tumescent swellings (stages 3 and 4), high-ranking males would replace the previous male and mate with the female (203 cases, unpublished data). Hence, low-ranking males were not able to stay close to receptive females after the call.

Grooming-mating exchanges

The mating period was particularly interesting as the number of males present and females simultaneously receptive often fluctuated throughout the period. Hence the ratio available males per receptive females varied from day to day and it was possible to determine its influence on females' grooming investments. Analyses revealed that receptive females groomed males longer when there were fewer available males in the group. This suggests that grooming-for-sex exchanges followed the market law of supply and demand and that the value of males could vary throughout time according to their availability. However, the multiple factors influencing grooming durations showed that not only supply and demand ratios determined the price of the exchange. Females also varied their grooming investment according to their receptive status. This seemed to contrast with previous results found in longtailed macaques in which swelling stages did not affect the way males valued females. In mangabeys however, if females exchanged grooming for mating when they were receptive, they groomed males significantly longer when they were at the first stages of their sexual cycles. The amount of grooming they gave was definitely higher than when they were not receptive, showing that the value females attributed to mating was higher than the value they attributed to receiving grooming. However, when females

displayed stage 4 swellings, their grooming investments decreased noticeably. This may suggest that females were conscious of their intrinsic value. A second effect may have also interfered with females' strategies to access males and multiply the mating: males' competition for access to receptive females. Indeed, when females displayed stage 4 swellings they were close to ovulation. Contrary to longtailed macaques, mangabey adult males reacted to the maximum tumescence and were shown to initiate the sexual activities. They would also engage in mate guarding females, reducing the other males' access. This males' form of sexual coercion (Smuts & Smuts 1993) would counteract female mate choice and it may not be so effective for females to invest in much grooming during this period.

Interestingly, from a situation in which competition for access to a partner is the norm to accomplish sex, grooming seems to facilitate the cooperative state of the partner. Indeed if males are not eager to engage in any sexual activities with females when they do not display maximum tumescence, they change their mind if grooming is part of the foreplay. Hence, sexual relationships in mangabeys form an interesting market paradigm in which females' strategies to multiple mating follow some of the biological market predictions. Females as well as males seem to accurately evaluate their immediate and fluctuating social environment and choose the amount of their investment on partners accordingly. Effects such as the availability of partners or their intrinsic value influence the way the exchanges are performed either in terms of grooming durations or in terms of grooming-sex sequence.

ACKOWLEDGEMENTS

We thank the Ministère de la Recherche Scientifique, the Ministère de l'Agriculture et des Ressources Animales, the CSRS, the CRE and the Taï Monkey Project in Ivory Coast for research permission and logistic support. We thank G. Gha, R. Peho and F. Range in Ivory Coast for assistance in the field. Max-Planck-Institut fuer Verhaltensphysiologie, CNRS and NWO (Evolution and Behaviour 051-12-036) provided financial support.

CHAPTER 6

Supply and demand determine the market value of food providers

Experiments in vervet monkeys

Cécile Fruteau, Bernhard Voekl, Eric van Damme, Ronald Noë

2009. Supply and demand determines the market value of food providers in wild vervet monkeys. PNAS, 106 (29), 12007-12012

C & JM Fruteau

ABSTRACT

Animals neither negotiate verbally nor conclude binding contracts, but nevertheless regularly exchange goods and services without overt coercion and manage to arrive at agreements over exchange rates. Biological market theory predicts that such exchange rates fluctuate according to the law of supply and demand. Previous studies showed that primates pay more when commodities become scarcer: subordinates groomed dominants longer before being tolerated at food sites in periods of shortage; females groomed mothers longer before obtaining permission to handle their infants when there were fewer newborns and males groomed fertile females longer before obtaining their compliance when fewer such females were present. We further substantiated these results by conducting a two-step experiment in two groups of free-ranging vervet monkeys in the Loskop Dam Nature Reserve, South-Africa. We first allowed a single low-ranking female to repeatedly provide food to her entire group by triggering the opening of a container and measured grooming bouts involving this female in the hour after she made the reward available. We then measured the shifts in grooming patterns after we added a second food container that could be opened by another low-ranking female, the second provider. All four providers received more grooming, relative to the amount of grooming they provided themselves. As biological market theory predicts, the initial gain of first providers was partially lost again after the introduction of a second provider in both groups. We conclude that grooming was fine-tuned to changes in the value of these females as social partners.

Trading in humans and cooperation in animals are part of a continuum in which both human and non-human agents usually have to take three crucial steps: (1) choose a partner, (2) determine how much to invest in order to obtain the desired commodities and (3) prevent being short-changed by the chosen partner. While research in economics traditionally concentrates on factors that determine the price of commodities, quantitative aspects have gained much less attention in studies of non-human cooperation (Noë 2005). Over the past decades, cooperation research has mainly focused on the question of partner control rather than on the relative values of goods and services exchanged. By contrast, the biological market paradigm (Noë & Hammerstein 1994, 1995) focuses on the link between steps (1) and (2) and predicts that the law of supply and demand affects the exchange rates in non-human 'trading' in a similar fashion as in human economic exchanges. Here we test this prediction in two wild vervet monkey groups by measuring changes in grooming patterns after experimentally changing the number of individuals that could provide food to their group.

We envisage the exchange of commodities in primate groups as trading on a market with exchange rates fluctuating from day to day depending on supply and demand. Monkeys trading goods and services have to agree on exchange rates in order to avoid overt conflicts, but lack the option of negotiating verbally and concluding binding contracts. Not all commodities exchanged among non-human primates can be adapted in quantity or quality during each interaction, but one service, grooming, can be adjusted easily. Grooming can be exchanged against grooming itself, but also against other goods or services, lending it currency-like characteristics. Commodities bought with grooming include tolerance at food sites (de Waal 1997; Barrett et al 2002; Henzi et al. 2003; Ventura et al. 2006; Chancellor & Isbell 2008; Port et al. 2008), access to newborns (Henzi & Barrett 2002; Gumert 2007a), compliance of females (Gumert 2007b), and support in conflicts (Hemelrijk 1994; Watts 2002; Koyama et al. 2006), although results on grooming-support exchanges have been mixed (Hemelrijk 1991; Silk et al. 2004; Schino 2007). Monkeys do not necessarily track value fluctuations for each commodity on the market separately, however,

but they may change their general attitude towards group members (de Waal 2000) in accordance with the accumulated value of the different commodities each one of them has on offer. Mechanistically the value attributed to a partner is likely to be expressed in physiological parameters such as titers of neurohormones and neurotransmitters implicated in trust and pair bonding (Keverne 1999; Kosfeld et al. 2005; Morhenn et al. 2008; Donalson & young 2008; Baumgartner 2008; Dunbar 2009).

We created an artificial market in two groups of wild vervet monkeys in the Loskop Dam Nature Reserve (South-Africa) and caused sudden changes in the market value of a few animals in such a way that these affected all other group members and could easily be perceived by them. After an initial phase in which we gathered baseline data on grooming (phase 0), we allowed a single low ranking female in each study group to produce a bonanza of food for herself and her group members by triggering the opening of a container in 16 trials spread over a period of 9 weeks (phase 1). These first two stages resemble a study previously done in captivity with long-tailed macaques (Stammbach 1988). In that experiment, a single individual that could produce a small food reward and share it with up to two other animals experienced an increase in social status. We developed this paradigm further to show the quantitative effects of a shift in supply on grooming patterns. This requires either a manipulation of the amount of reward per provider or of the number of providers. We opted for the latter approach since it is very hard to control the amount of food each individual will obtain once the provider made it available. In phase 2 of the experiment we therefore introduced a second provider in each group, another low ranking female with a second food container that only she could open. The same amount of food (5 apples per trial sliced in small pieces) was now divided over the two containers that were made available simultaneously, but that were not necessarily opened simultaneously. In economic terms we thus replaced a monopoly by a duopoly. Agents enjoying a monopoly should obtain stronger leverage over their exchange partners than members of a competitive duopoly. This leads to our main prediction: grooming ratios should increase in favor of the provider in phase 1 and decrease again

with the introduction of a competitor in phase 2, as depicted in Fig. 1A. We used the ratio of grooming given relative to grooming received as our main parameter, because we expected that group members could pay the providers both by grooming them more and by demanding less grooming from them.

There is considerable discussion about the function of grooming in primates. A first basic assumption is that grooming entails a net cost to the groomer and provides a net benefit to the groomee. In free-ranging groups, grooming is very likely to have an opportunity cost in the form of lost foraging time and lowered vigilance (Lehmann et al. 2007). Captive animals, in contrast, sometimes groom excessively, out of boredom, or in the form of a pathological stereotypy, thus removing the incentives to reduce grooming payments to a minimum. However, even in the wild primates groom each other much more than can be explained by its hygienic function, the most likely ultimate function of allo-grooming (Dunbar 2009). The proximate mechanisms that make monkeys enjoy being groomed include the release of several neurotransmitters and neurohormones implicated in the brain's reward circuit, analogous to the reaction of human subjects to touch (Morhenn et al. 2008; Dunbar 2009). Enjoying being groomed is a bit like enjoying eating: the proximate mechanisms are such that the system easily overshoots the original ultimate goals. Additional functions may be served, such as building up fat reserves when eating, or strengthening the bonds between individuals when grooming. In primates the latter is now probably more important than the hygiene of the fur (Dunbar 2009). The crucial question here is not, however, what the exact function of grooming is, but whether grooming is sufficiently costly to underlie market forces, in the sense that animals prefer grooming another animal shorter rather than longer if the effect remains the same. We follow the tradition of estimating the amount of grooming by the length of time a grooming bout lasts. Although the value of a unit of grooming time may drop as the grooming bout progresses, it seems safe to assume that longer bouts have higher value than shorter ones within the same dyad. Expressing the value of grooming in time units also makes our results more easily comparable with a recently published formal market

model that used time units to express the value of services (Lehmann et al. 2007). We felt confident that grooming patterns underlie market forces, since market effects had already been shown in several studies apart from our own (Henzi & Barrett 2002; Ventura et al. 2006; Gumert 2007a, b; Chancellor & Isbell 2008; Port et al. 2008).

We chose low ranking females as providers, since lower ranking individuals in primate species with clear dominance hierarchies tend to groom higher-ranking members of their group more than vice versa (among others Barrett et al 2002; Henzi et al. 2003; Barrett & henzi 2006; Chancellor & Isbell 2008; Port et al. 2008; Fruteau et al. in prep.). The reason behind this is that a dominant individual can offer several resources, apart from grooming, that the subordinate cannot match in value: support in agonistic conflicts, tolerance at resources or even simply restraint in aggression. We therefore expected to see much stronger effects in low ranking providers than in high-ranking ones.

What exactly are our providers offering their group members? Each provider opened a container with enough pieces of apple to give every group member a good chance of getting hold of some food in a free-for-all determined mainly by dominance. At first sight, providers would not seem able to give food to some members more than to others. This means that partner control strategies, such as reciprocal altruism (Trivers 1971) or tit-for-tat (Axelrod & Hamilton 1981) cannot play much of a role. Reciprocal altruism has been construed in a narrow and in a broad fashion. Models using the narrow interpretation, which are usually based on variations of the two-player iterated prisoner's dilemma, allow precise predictions about the behavioral contingencies of two partners in repeated interactions. The few studies in which these predictions have been tested in primates yielded negative results (Mellis et al. 2008; Brosnan et al. 2009). This narrow interpretation does not apply to our experiment, because *a priori* our providers cannot make a strategic choice that is simultaneously contingent on behavior of group members that treated them differently in the previous 'round'.

In a much broader interpretation, reciprocal altruism encompasses all forms of partner control mechanisms in which individuals reward or punish their partners on the basis of past behavior. One way in which our providers could give some group members an advantage over others is by making the timing of opening contingent on the past behavior of the group members near the container, assuming that being near gives a competitive advantage. This way the provider could, to a limited extent, individualize the commodity offered. This still does not mean that providers can play dyadic games with all their group members simultaneously, but they could exert some partner choice this way. Partner choice is the core mechanism driving biological markets, but is not taken into account in reciprocal altruism and other partner control models.

In summary, these considerations lead us to expect: (i) baseline grooming ratios to be skewed in favor of more dominant individuals; (ii) grooming patterns to change strongly in favor of the first providers, but to become less favorable again when the second providers are introduced; (iii) providers to open the containers preferably in the presence of those grooming them most.

RESULTS

The grooming ratio can shift in favor of a provider in several ways: either the provider can groom less or her group members can groom her more, or both. It is perhaps easier to adjust a grooming ratio to one's own advantage by grooming less than by persuading the other to groom longer, but this does not warrant strong predictions about shifts in absolute grooming bout lengths. We therefore used grooming ratios per dyad, calculated as time-being-groomed minus time-spent-grooming divided by total-grooming-time, which yields values between -1and 1. In the experimental phases, grooming data were recorded during one hour after the containers were opened. We had expected to see changes in grooming patterns before the containers were opened too, but in practice we could not measure this. Early in the series of trials the animals were too excited to sit down for a grooming session with food visible in the closed container and at a later

stage the providers often opened the containers almost immediately, leaving no time for grooming sessions (see table S1 in the supporting information).

In the pre-experimental phase 0 we measured baseline grooming ratios, which were highly correlated with the relative rank difference of the corresponding dyads (Mantel Test (de Vries et al. 1993), combined probabilities (Sokal & Rohlf 1995): χ^2=25.69, p<0.001), i.e. the larger the rank difference, the more lopsided the grooming effort was in favor of the dominant.

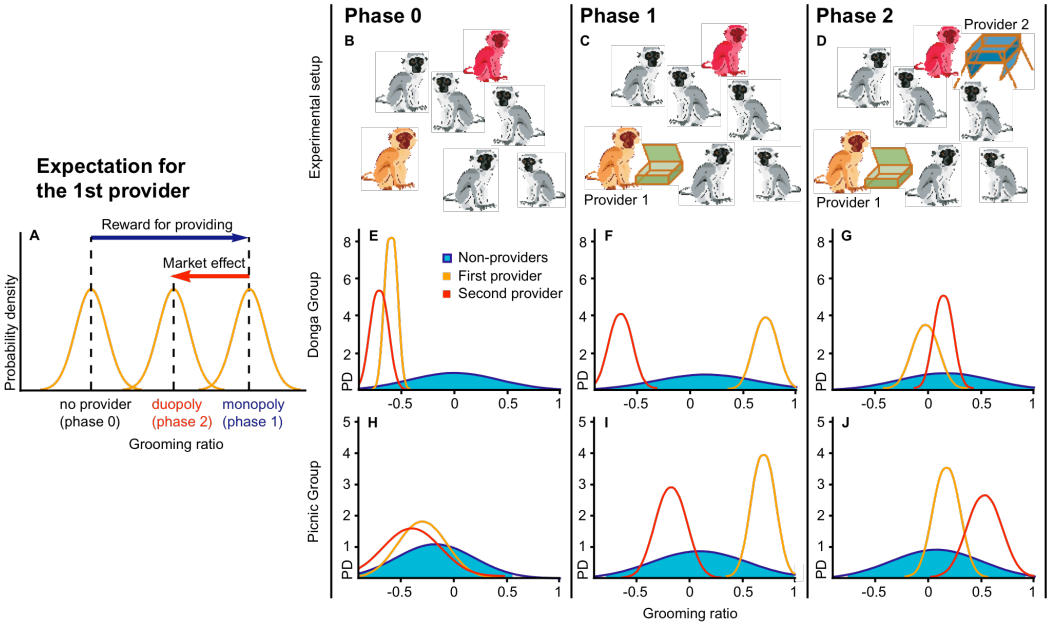


Figure 1. Mean estimates of the grooming ratios for the food provider. Expected effects (A). In phase 0 of the experiment each individual has a specific grooming ratio of grooming received versus grooming given. In phase 1 (monopoly) the grooming ratio of the single food provider should increase (reward for providing). But, as soon as an additional provider is introduced in phase 2 (duopoly), the grooming ratio of the first provider should decrease again as a consequence of the increased supply of food providers (market effect). Schematic representation of the three experimental phases (B-D). Probability density (PD) function of mean estimates for grooming ratios of non-providers (blue), first provider (orange) and second provider (red) in phase 0 with no provider (E,H), phase 1 with one provider (F,I) and phase 2 with two providers (G,J) for the Donga Group (E-G) and Picnic Group (H-J).

The grooming ratios of the providers differed significantly among the three phases (Friedman Test, combined probabilities, first provider: χ^2=26.25, p<0.001, second provider: χ^2=18.59, p<0.001). After showing that the overall experiment yielded a highly significant result, we proceeded with a number of post-hoc Sign tests. The grooming ratios for the first providers in

each group changed according to expectation (Fig. 1A): the ratio increased significantly in favor of the provider from the non-test phase 0 to test phase 1 (single provider; χ^2=15.25, p<0.01). Grooming ratios for the first provider dropped significantly again when the second provider was added in phase 2 (χ^2=15.25, p<0.01), but remained significantly above the control values of phase 0 (χ^2=15.25, p<0.01). As expected, the grooming ratios for the second providers did not change significantly between phase 0 and 1 (χ^2=3.54, ns), but their ratios shot up when they became providers themselves in phase 2 (χ^2=15.25, p<0.01). The provider effect was so strong that it more than counterbalanced the dominance effect. The strongly negative grooming ratios of the low ranking females we measured in phase 0 turned into positive values once they became providers. To evaluate whether these changes for providers were indeed outside the range of fluctuations found in the non-providers (e.g. as due to seasonal changes), we estimated mean changes in grooming ratios for both providers and non-providers using a hierarchical bootstrap re-sampling procedure to deal with dependencies among dyads (Efron 1982) (Fig. 1 I-J). The differences in grooming ratios between the non-test phase 0 and phase 1 were significantly greater for the first providers than for the group of non-providers (Donga Group: p< 0.0001, Picnic Group: p=0.0005, combined probabilities: χ^2=54.65, p<0.001). Grooming ratios increased significantly for both second providers compared to the non-providers in phase 2 (Donga: p<0.001, Picnic: p=0.040, combined probabilities: χ^2=102.72, p<0.001). Comparing grooming differences between the non-test phase and phase 2 we found a significant difference between the first provider and the group of non-providers in the Donga Group, but not in the Picnic Group (Donga: p=0.0029, Picnic: p=0.91, combined probabilities: χ^2=11.90, p<0.025).

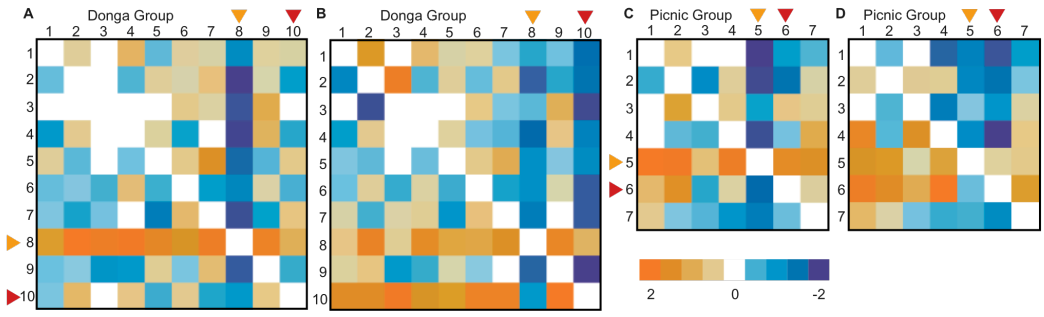


Figure 2. Changes in dyadic grooming ratios. Difference between phase 1 and phase 0 for Donga Group (A), and Picnic Group (C), and difference between phase 2 and phase 0 for Donga Group, (B), and Picnic Group (D). Individuals are ordered by rank; 1 = highest ranking animal. Rows: groomers, columns: groomees. Values were calculated by subtracting grooming ratios of phase 0 from those of phase 1 or 2 respectively. As original ratios were ranging between -1 and 1, differences could range between -2 (blue; maximum shift in favor of groomer) and 2 (orange; maximum shift in favor of groomee). First providers are indicated by orange arrows and the second producers by red arrows.

These changes in grooming ratios were not due to a change in behavior of a few individuals, but visible in a broad range of dyadic relationships (Fig. 2). In 13 out of 15 dyads the providers groomed less in an absolute sense, compared to the pre-experimental phase. In four dyads, two in each group, the non-providers groomed the providers more. Three of these four were among the 13 in which the non-providers were groomed less.

We also verified whether providers attempted to give specific individuals a head start by opening the container preferentially in their presence. They could be expected to do so for two classes of individuals: (1) long-term friends or kin with whom they had a positive relationship and (2) animals that groomed them specifically in the context of the trials. Providers did not open the containers preferentially when their preferred grooming partners from phase 0 were nearby (Donga Group: Spearman Rank Correlation: 1st provider: r_s=0.31, N=9, n.s., 2nd provider: r_s=0.52, N=9, n.s.; Picnic Group: Spearman Rank Correlation: 1st provider: r_s=0.13, N=6, n.s., 2nd provider: r_s=-0.25, N=6, n.s.), but in both groups we found, in phase 1, that an individual that happened to be the nearest neighbor at the moment of opening was significantly more likely to groom the provider (single provider; Donga Group: χ^2=33.69, df=9, p<0.001; Picnic Group:

χ^2=13.5, df=6, p=0.036; combined probabilities: χ^2=25.06 df=4, p<0.001). During test phase 2, this effect was also found for the first providers (combined probabilities for the 1st providers of both groups: χ^2=10.33, df=4, n.s.), but not for the 2nd providers (combined probabilities for the 2nd providers: χ^2=6.38 df=4, n.s.). Thus, the first providers were likely to be engaged in grooming sessions with individuals that were near the container when it opened and thus probably got more food than latecomers (see Supporting Information for details of statistical tests).

DISCUSSION

In agreement with an earlier study (Stammbach 1988), we found that grooming ratios shifted to the advantage of female vervets that produced food bonanzas. Our crucial result, however, lies in the quantitative shifts of the exchange rate between grooming and providing food: the positive effect on the grooming ratios of the first providers was roughly half as strong after we added a second provider in each study group, confirming a central tenet of biological market theory (Noë & Hammerstein 1994, 1995; Lehmann et al. 2007). Similar market effects have hitherto only been reported for primates exchanging grooming for access to naturally occurring commodities (Barrett et al 2002; Henzi & Barrett 2002; Henzi et al. 2003; Gumert 2007a, b; Chancellor & Isbell 2008; Port et al. 2008).

Grooming ratios were adapted rather quickly to changing circumstances and we therefore assume that this reflects strategic behavior that forms part of the natural repertoire of vervets. Allowing some animals to produce food sources for themselves and their group members by opening a container is obviously rather artificial. However, it is not necessarily uncommon or unnatural for a primate group to gain access to a large food source thanks to a single group member. Two phenomena come to mind: animals giving a food call after finding a large resource (Dittus 1984; Elgar 1986; Chapman 1990; Calne et al. 1995) and experienced ‘leaders’ (King & Cowlishaw (2009) guiding their group to crucial resources (Rowell 1972;Norton 1986; Byrne 2000). Neither phenomenon is found in all primates, or unique to primates, but both are

sufficiently common to make the existence of mechanisms encouraging food providers likely. Our providers might be comparable to leaders, which in primates can be high as well as low ranking females (RN pers. obs. in savannah baboons; Norton 1986; Byrne 2000), since in both cases the same individual produces a communal resource repeatedly, thus giving their group members time to recognize their special skills. In all three cases, food calls, leading and our experiment, the animal producing the resource may act on purely selfish motives. Leaders and providers may forage for themselves and produce food for others as a by-product and food calls might only be given upon finding large and shareable resources to protect the caller against predators by improving the 'safety-in-numbers' (Elgar 1986; Mangel 1990; King & Cowlishaw 2009).

A provider can be expected to open the food container sooner or later out of pure self-interest, as long as she gets some food herself without experiencing unusual harassment. Why would group members pay for something they would obtain by simply waiting long enough? We assume that vervets, like many other animals, discount future benefits and value a reward more the sooner it becomes available (Stevens & Stephens 2008). In addition there was a clear opportunity cost of waiting near the closed food container, because the group could not continue its normal foraging routine.

It seems reasonable to assume that only a limited amount of grooming - irrespective of who provides it - is needed to induce the providers to open their containers. In that case, each of the non-providers would have been better off if others provided all the grooming needed. The non-providers would thus be caught in collective action dilemma, a situation that resembles the notoriously unstable n-players Prisoner's Dilemma (Rankin et al. 2007). So why did the whole group change its grooming behavior to the advantage of the providers or, in other words, how could an individual willing to groom the provider do better than an animal that did not groom her?

The provider could make the timing of opening dependent on the presence or absence of specific group members. The providers were indeed reluctant to open their container in the presence of high-ranking animals (Fruteau et al. in prep.). Providers were also more likely to be

groomed by non-providers that were near the containers at the moment they were opened than by non-providers that were further away. We see four, not necessarily mutually exclusive, interpretations of this phenomenon: (1) those that ate more during a trial were more inclined to groom; (2) grooming improved long term bonds and the providers preferably opened the containers in the presence of group members they trusted; (3) grooming and opening the container were exchanged in a reciprocal altruism-like fashion and (4) grooming ratios reflected the stress level of the providers rather than their market value.

(1) Grooming sessions often follow longer periods of foraging. A simple explanation would therefore be that those with fuller bellies were inclined to groom more. This can explain more grooming by those that obtained most of the resource, such as the provider and others near the container at the moment of opening, but this cannot explain the shifts in grooming ratios we observed.

(2) Non-providers could have groomed the provider in order to improve their affiliative bond with her. Candidate neurobiological mechanisms are those usually connected to trust, pair-bonding and friendship, such as increased titers of oxytocin, vasopressin and endorphins, which notably follow friendly forms of touching (reviewed in Baumgartner 2008; Donalson & Young 2008). The attitude towards a group member can be improved by any good or service received from that individual, but grooming is the standard service every vervet has handy.

Grooming to gain trust reminds of a mechanism De Waal (2000) labeled 'attitudinal reciprocity', which stands for a generalized bookkeeping mechanism based on multiple interactions in which the more recent interactions tend to weigh more than those from a more distant past. 'Attitudinal partner choice' would be more accurate term in the present case, but the idea remains the same: the animals are assumed to be driven by emotions reminiscent of those felt by humans towards friends.

(3) Grooming the provider can also be interpreted as contingent on the provider's behavior, in other words the provider is pre-paid in the expectation of returns during the next trial. This would

imply a more accurate form of bookkeeping in the sense of De Waal's 'calculated reciprocity' (2000) and would suggest cognition to be in the driver's seat. For this reciprocal altruism-like mechanism to work the groomers must have been willing to invest in a future reward that could be reaped one or more days later. Investments in uncertain returns over such long periods could be beyond the cognitive capacities of monkeys, however (Barrett et al. 2003). Calculating providers should have been ready to take spiteful decisions: not opening the container would have punished individuals that were not willing to shift the grooming ratios in favor of the provider, at a cost of the provider herself and those who groomed her. Alternatively the provider could have punished specific individuals by waiting till they were at some distance from the container. It is highly unlikely that our providers used this rather complicated tactic, however, because they opened the container almost immediately in the later trials (Table S1 in online material).

(4) An explanation for dynamic changes of primate grooming patterns that does not invoke the law of supply and demand (Henzi & Barrett 2002; Slater et al. 2007) is based on the idea that the proximity of group members causes stress to those controlling interesting commodities. More attention would cause more stress, which in turn would require more grooming to calm the provider. This stress hypothesis has notably been suggested for 'baby markets': the level of anxiety of mothers would increase with the number of females vying for their infants simultaneously and the amount of grooming needed to calm her would increase accordingly (Henzi & Barrett 2002; Slater et al. 2007). However, the stress hypothesis also predicts that high-ranking handlers, who cause more stress (Sapolski 2005), would have to groom longer than low ranking ones. The opposite was found, however (Henzi & Barrett 2002; Gumert 2007a; Port et al. 2008, Barrett & Henzi 2006), which makes sense from a market perspective: high-ranking individuals can compensate low amounts of grooming by offering tolerance, restraint and/or support, which all have higher value the higher-ranking the donor is. In our study higher-ranking individuals also groomed the commodity providers less than lower-ranking ones (Fruteau et al. in

prep.). Moreover, in the relaxed period after the consumption of the reward during which we measured grooming times, the providers were no longer under extraordinary attention.

The question remains whether the grooming patterns observed after the containers were opened could indeed be interpreted as rewarding and/or pre-paying the providers. Not all group members groomed providers more; some also accepted shorter grooming bouts from the providers compared to the pre-experimental phase. Again this makes sense if one thinks in terms of mechanisms of price setting in a market: during a grooming session both partners can test their momentary market value by ending a grooming bout and monitoring their partner's reaction. Providers were probably confronted with less dissatisfaction if they groomed others only briefly, while at the same time their own signs of dissatisfaction carried more weight. A price setting process is dynamic and grooming ratios can thus be adjusted in several ways: one party grooms less, or the other grooms more, or both.

In conclusion, the adjustment of grooming ratios can be understood as a continuous bargaining process in which bargaining positions depend on the perception of the other's value as a partner in a long-term perspective. Grooming plays a dual role in this process: it functions both as a currency, because of its direct influence on the reward system of the groomee and as a commodity, because it can be traded directly for access to infants, tolerance and so forth too. Grooming can thus be used to balance asymmetries in trades of other commodities. In our experiment this balance shifted suddenly, and grooming patterns were quickly adjusted, when we experimentally created a monopoly and shifted again when we turned the monopoly into a duopoly. Thus, free ranging monkeys can accurately adjust to shifting markets, although they cannot rely on language for bargaining and have no obvious way of concluding binding contracts.

METHODS

Observer team

The observer team consisted of the first author and seven different assistants: E. van de Waal: 09/2005 - 01/2006; S. Lemoine: 02 - 05/2006; V. Dufour and S. Aubel: 05 -06/2006; E. Hellard and A. Brotz: 06 - 08/2006; E. Hellard and D. Carter: 09/2006.

Research area and subjects

We used two free ranging vervet monkey groups, *Chlorocebus aethiops*, in the Loskop Dam Nature Reserve, Mpumalanga Province, South Africa. Loskop is located at 180 km north-east of Pretoria, covers approximately 25000 ha, is on average 1000 m above sea level and consist mainly of 'bushveld' (tall grasses and thick acacia bushes). Winters (May-October) are dry and cold and summers (November-April) are hot and humid.

Both study groups were habituated to human observers prior to the start of the experiments. Their home ranges of approximately 3 km^2 each were about 3 km apart. The Donga Group had a period of fast turn-over of adult males prior to the study period but the total group size never exceeded 15. We observed three to five adult males, seven adult females, one to two sub adult individuals and one to two infants at a time. The Picnic Group had two to three adult males, four adult females, one juvenile and two to six infants at a time. The dominance hierarchies remained stable throughout the study period. For the experiment, we selected the two lowest-ranking females that would accept manipulating the containers as food providers.

Experiment protocol

The experiment had three phases: a period without a provider, (phase 0, September 2005 – April 2006, 221 observational sessions for Donga Group and 191 for Picnic Group, of which we randomly chose 55 sessions per group for analysis), a period with 1 provider per group (phase 1, May to June 2006, 16 trials per group, always the same female as provider) and a period with 2

providers per group (phase 2, August-September 2006, 22 tests per group, the same first provider plus a second one). Both experimental phases were preceded by a period of training in which the providers learned to touch the lid of their specific food container.

The groups were followed every second day during phase 0 and two days in a row every four days during the two testing phases 1 and 2. In phases 1 and 2 we waited until the animals reached a suitable area (open with big trees nearby for the vervet monkeys to rest safely) before positioning the food container. After a provider opened the container we recorded all grooming interactions within the following 60 minutes. Each approach and opening of the containers by the providers was recorded with digital video cameras (Samsung VP-D361i and Panasonic NV-GS11). One observer (CF) continuously followed the provider while two assistants recorded the interactions of the rest of the group. All agonistic and affiliative interactions were recorded continuously (Altmann 1974) and the distance between every visible vervet and the experimental containers was recorded in 30 s intervals. Grooming bouts were timed to the nearest second. A bout was considered to have ended when either the direction of grooming changed or when there was a break of more than 20 seconds. A trial was aborted if one or both of the providers did not open her container during one hour, which happened five times in phase 2 for Donga Group and once in phase 2 for Picnic Group. The procedure for phase 2 was identical to the trials in phase 1, except that two containers were placed simultaneously at about 2 m distance from each other. The reward was the same as in phase 1 and evenly distributed over the two containers. Both providers were followed by one observer, each, while a third observer recorded the interactions between the remaining members of the group.

Observations were distributed throughout the day but the majority of the data was taken from 6 a.m. to 1 p.m. and from 4 p.m. to 6 p.m. We used Pendragon Forms (professional edition 4.0.00) on Palm Zire 31 handheld computers for all behavioral data. Births, immigrations, disappearances and intergroup encounters were recorded on a daily basis.

Food containers

We worked with two containers (50 x 55 x 15 cm) with wooden frames that were both covered with a plastic mesh on all sides and reinforced with a metallic grid on top allowing the vervets to see and smell the food (Fig. S1A). The second container stood on 50 cm legs and had a split bottom, causing the food to drop to the ground (Fig. S1B). The containers were filled with total of 5 chopped apples per test. This was sufficient to ensure that most adults got a share. The obvious differences in form and color made it easy for both providers and non-providers to attribute a specific device to a specific provider. The containers were unlocked by remote control (a car door locking device) as soon as the provider touched the lid.

Training of providers

To habituate all animals to the food containers and to train the providers to operate them, we conducted a training phase with 24 trials per group from October 2005 to mid-January 2006 for the first providers and a training phase with 12 trials per group for the second providers in July 2006. We provided five chopped apples per trial and we opened the container by remote control as soon as the selected provider touched it. The trials were not time restricted, i.e. we waited until the providers dared to come and open their container. During the first training phase, dominant individuals tried to monopolize the food as soon as the container was opened, which lead to serious harassment of the low ranking providers. We placed two extra apples (also cut into pieces) outside the container as soon as the provider had opened the container to reduce this harassment. This additional food supply was not necessary for the second training phase, where harassment of the providers was much lower. It took only one trial for three of the providers to come to touch the container by chance. The 2nd provider of the Donga Group touched the container for the first time in the 5th trial. Throughout the training phases, the time required by the providers to open their container dropped quickly: First providers, Donga Group: from 35 minutes to less than 1 minute, Picnic Group: from 120 minutes to less than 10 minutes; second providers: Donga Group from 55

minutes to less than 2 minutes, Picnic Group: from 75 minutes to less than 10 minutes. None of the providers attempted to open the container attributed to the other provider after the training phase.

Statistical tests

We give only combined probabilities for both groups whenever the same effects were found in both. Raw data and separate probability estimates are given in the supporting tables S1- S5. Rank order and linearity indices were determined with the MATMAN software (de Vries et al. 1993, all other computations were made with MATHEMATICA 6.0 (Wolfram Research 2007).

ACKNOWLEDGEMENTS

We thank the Mpumalanga Parks Board, UNISA and ABEERU colleagues, L. Brown, L. Barrett, S. P. Henzi and R. Bshary, for research permission and logistic support. S. Aubel, A. Barrett, A. Brotz, D. Carter, V. Dufour, E. Hellard, S. Lemoine and E. van de Waal assisted in the field. Suggestions by R. Bshary, S.P. Henzi, R. Johnstone, K. Zuberbühler , the editor and three anonymous referees improved the paper significantly. CNRS, NWO (Evolution and Behaviour 051-12-036), and EU-FP6 (GEBACO 28696) provided financial support.

Supplementary online information

Videos showing examples of experiments are made available online.

Training of the providers

To habituate all animals to the food containers and to train the providers to operate them, we conducted a training phase with 24 trials per group from October 2005 to mid-January 2006 for the first providers and a training phase with 12 trials per group for the second providers in July 2006. We provided five apples, each cut into 24 pieces, per trial and we opened the container by

remote control as soon as the selected provider would touch it by chance. The trials were not time restricted, i.e. we waited until the providers touched their container. During the first training phase, high-ranking individuals tried to monopolize the food as soon as the container was opened, which lead to serious harassment of the low ranking providers. We placed two extra apples (also cut into 24 pieces) outside the container as soon as the provider had opened the container to reduce this harassment. This additional food supply was not necessary for the second training phase, because the dominant animals had learned to keep their distance by then (Fruteau et al. in prep.). It took only one trial for three of the providers to come to touch the container by chance. The 2nd provider of the Donga group touched the container for the first time in the 5th trial. Throughout the training phases, the time required by the providers to open their container dropped quickly: First providers, Donga group: from 35 minutes to less than 1 minute, Picnic group: from 120 minutes to less than 10 minutes; second providers: Donga group from 55 minutes to less than 2 minutes, Picnic group: from 75 minutes to less than 10 minutes.

Comparison of food containers

For the experiments we used food containers with different opening mechanisms (top opening and bottom opening, see Supporting Fig. 1). However, these different mechanisms did not seem to cause differences in the access to the reward in terms of numbers of individuals accessing it (mean ± SE, N = 22: Donga first container: 2.5 ± 0.22 individuals; Donga second container: 2.4 ± 0.19; Picnic first container: 4.4 ± 0.33; Picnic second container: 4.6 ± 0.46) or the time each individual could forage (mean ± SE, N = 22: Donga first container: 132 ± 26.4 s; Donga second container: 132 ± 24.6 s; Picnic first container: 102 ± 19.2 s; Picnic second container: 96 ± 17.4 s).

Food competition test

The natural frequency of interaction in small groups of vervet monkeys is very low. Hence, to evaluate the rank hierarchy of the adult animals we used dry maize (distributed widely to prevent

violent interactions) to conduct 20 food competition tests per group from September 2005 till May 2006. The tests lasted until all adult animals came to feed (from 60 to 120 minutes). For the socio-matrix we only used the recorded approach/retreat and threat/retreat unidirectional interactions to determine the subordinate individual of each dyad. In both groups the rank-order among adults was strictly linear (Kendall's coefficient of linearity K=1 in both groups, combined probability: χ^2=30.75, p<0.001) and did not change in course of the experiment.

Proximity to providers

Those individuals that are closest to the container when the provider opens it and, hence, have the shortest latency to reach the container are likely to profit most. Such individuals could have paid more by grooming relatively more afterwards. Alternatively, the provider could have opened in the presence of individuals with whom she generally had a strong affiliative relationship. Thus, we performed two statistical tests: (1) comparing the grooming activity involving the providers in phase 0 (with no experimental manipulation) with proximity to the provider in the test phases, and (2) comparing whether individuals that were near the container at the moment it was opened were grooming the provider more often than when they were not nearby. In cases where two animals were approximately equally close to the provider, both were scored as nearest neighbours to avoid an unconscious observer bias. Comparing the total grooming times involving the providers in phase 0 with the frequencies of being nearest neighbour to the provider during opening we found no significant correlation for both providers of group Donga (Spearman Rank Correlation: 1st provider: r_s=0.31, N=9, n.s., 2nd provider: r_s=0.52, N=9, n.s.) nor for group Picnic (Spearman Rank Correlation: 1st provider: r_s=0.13, N=6, n.s., 2nd provider: r_s=-0.25, N=6, n.s.). Due to the low power of these tests the missing significances should be interpreted very carefully, but we can safely say that there was no strong relationship between grooming in the baseline condition and being nearest neighbour. To determine whether individuals that were near to the provider (and consequently also near to the container) during opening were grooming the provider more often

than when they were not near to her, we used a replicated goodness-of-fit test based on the G-statistic (Sokal & Rohlf 1997). Individuals groomed the provider more often when they were nearest neighbours during the opening event than when they were not during test phase 1 (Donga: χ^2=33.69, df=9, p<0.001; Picnic: χ^2=13.5, df=6, p=0.036; combined probabilities: χ^2=25.06 df=4, p<0.001) but during test phase 2 this effect was also found for the first providers (combined probabilities for the 1st providers of both groups: χ^2=10.33, df=4, n.s.), but not for theh 2nd providers (combined probabilities for the 2nd providers: χ^2=6.38 df=4, n.s.). The significant results cannot be explained by simple proximity effects, because we measured grooming in the hour after a container was opened and thus after almost all animals had been close to it. The provider could in principle also have been groomed by animals interested in being close at the time of opening immediately before the trial started, i.e. after the experimenters handled the material. We were unable to measure grooming while preparing the trial, but the animals were generally exited and did not groom much.

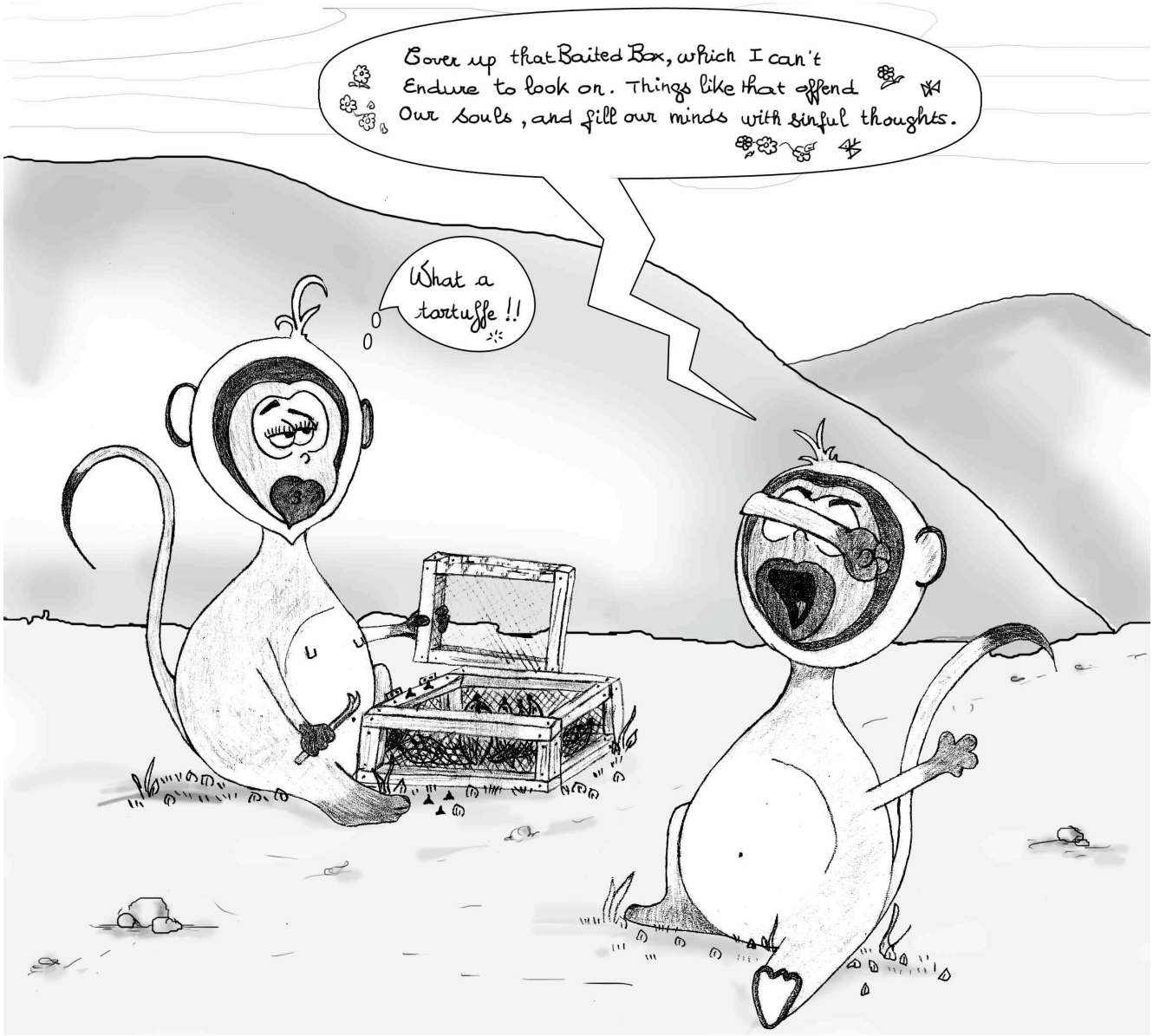
References

Sokal RR, Rohlf FJ (1995) Biometry. New York: Freeman.

CHAPTER 7

Queuing-to-learn self-control in wild vervets
Learning mechanisms and memory

Cécile Fruteau, Erica van de Waal, Nicolas Poulin, Eric van Damme, Ronald Noë



C & JM Fruteau

ABSTRACT

In the course of testing some of the law prevailing in the biological market theory, we performed food production experiments in two groups of free-ranging vervet monkeys. The experimental set up, allowing low-ranking females to become food-providers, was heavily disturbed by highest-ranking individuals monopolising the closed containers and preventing the providers from opening them. However, highest-ranking individuals quickly learned to inhibit their aggressive monopolization by deliberately moving away from the containers hence, reducing the frequency of conflict occurrence toward the providers in the process. We found that the learning mechanisms were made over few trials. We demonstrated that high-ranking individuals used the outcome of the five previous trials to choose the adequate behaviour and each learnt in turn. This queuing process along with the fact that each next individual seemed to learn faster than the previous one, lead us to assume that the learning processes may be enhanced by sociality. We also found that the providers used their past experience to choose the best moment to open the container. Our overall impression was that the providers' group members behaved in such a way that tensions were lowered and containers opened more quickly. Although self-control has been the topic of several studies in captivity recently, it has essentially been explored in term of individual cognitive capacities and not in term of social relationships. Hence, our study is the first to report self-control in both wild and social conditions and to give evidence of the learning mechanisms.

The fact that individuals gather together and form long lasting relationships is often explained in term of the advantages such social groups are providing. To name but a few, safety from predation through dilution effect (Bertram 1978) and increased foraging efficiency thanks to information sharing (Hamilton 1971; Ward & Zahavi 1973) both add to individuals' survival and fitness. However living in group also has its share of inconvenience (Krause & Ruxton) such as competition for food and scrounging, i.e. 'individuals usurping the resources found by others' (e.g. Ranta *et al*. 1996). Within groups, public information as well as hierarchical relationships influence the way resources are exploited and individuals may usually differ in their investment for foraging activities. For instance, in most species high-ranking individuals can easily displace others from food patches and are thought to be rather good candidates for learning how to recognise foraging success cues and for actively scrounging (Barnard & Silby 1981; Templeton & Girardeau 1995).

In primates, high-ranking individuals often display both priority of access and aggressive resource protection behaviours (Pruetz & Isbell 2000; diBitetti & Janson 2001; Witting & Boesch 2003), especially in food contexts. Hence, experiments relying on food production by low-ranking subjects (Stammbach 1988) may prove difficult to set up with free-ranging groups for which isolating individuals as it is done in captive conditions, is not an option. The recent development of the biological market theory (Noë & Hammerstein 1994, 1995) however, conducted many researchers to reconsider cooperative and mutualistic actions nature wide (mycorrhiza associations: Schwartz & Hoeksema 1998; rhizobia associations: West *et al*. 2002; Denison 2003; obligate pollination mutualisms: Pellmyr & Huth 1994; Fleming & Holland 1998; cleaner fish - client reef fish associations: Bshary2002; Bshary & Grutter 2002, 2006) and in the course of testing some of the law prevailing in the biological market theory, we performed food production experiments in two groups of free-ranging vervet monkeys (Fruteau *et al*. 2009). We desired to investigate the currency functions of grooming when one and then two low-ranking females were giving the opportunity to open containers filled with apples, hence supplying the whole group

with appetent food. Since these food production experiments by subordinates required to be done with wild animals, scrounging and aggressive behaviours represented negative parameters preventing low-ranking individuals to first access the food source and to be tolerated around it. The relatively easiness in the performance of the experiments was rather unexpected and reminded us of self-control behaviours.

If self-control as well as patience have been tested in many primate species, experiments were done in captive conditions in which subjects were isolated from their social group during the course of the testing session. Reverse-reward contingency experiments, in which subjects were learning to choose the smaller of two rewards in order to obtain the biggest, simulated self-control conditions (chimpanzees: Boysen & Berntson 1995; Boysen et al. 1996; macaques: Tobin et al. 1996; squirrel monkeys: Anderson 2000; orang-utans: Shumaker et al. 2001; tamarins: Kralik et al. 2002; lemurs: Genty et al. 2004). In a similar way, temporal discounting experiments in which individuals had to choose between an immediate but small reward and waiting a variable amount of time for a larger reward submitted subjects to patience (tamarins and marmosets: Stevens et al. 2005 b; capuchins: Ramseyer et al. 2006; chimpanzees: Dufour et al. 2007). Self-control and patience were therefore explored through the scope of individual cognitive capacities but not really in term of social relationships among group members. In the wild, examples of both self-control and patience are not so widely observed and even less tested. There are examples of males temporally inhibiting aggressive behaviours toward receptive females around food patches or the case of the Japanese macaque female that learnt to momentarily loose dirty wheat seeds by throwing them in water in order to clean them from their sandy crust (Kawai 1965). In this study however, some of the vervet monkeys' behaviours seemed to provide first hand data on primates' self-control in wild conditions as well as on the likely learning mechanisms permitting the emergence of self-control.

Learning mechanisms can usually be divided it two categories. One category operates when individuals experiment new food or situations in a solitary fashion, such as trial-and-error

learning (e.g. Thorpe 2008 for a review of learning capabilities recorded in wild birds). Trial-and-error learning mechanisms (Thorndike 1911 reviewed in Pearce 2008) imply that animals would behave randomly until they do something in the direction of the solution, are rewarded and by bits and pieces perform the correct answer to solve the task. Then the effect of the reward would strengthen the accidental answer and increase its occurrence in the future (Law of Effect, Thorndike 1911). However many researchers have argued that animals may be more sophisticated in their learning mechanisms that primarily suggested by the Law of Effect (e.g. Köhler 1925; Premack 1976; Epstein et al. 1984). They suggested that animals might have a better understanding of the causal implications of a behaviour and its consecutive outcome. Some suggested animals also had insigh (e.g. Köhler 1965) now referred to as causal relationships understanding (e.g. in primates: Visalberghi & Trinca 1989; Sabbatini & Visalberghi 2008), which would be identified by a brusque change in behaviour leading to the solving of a problem.

The other category of learning mechanisms, social learning, requires a social environment, and includes observational learning (e.g. Curio 1988; Mineka & Cook 1988), mimicry (e.g. Goodall 1986; Russon & Galdikas 1993), emulation (Tomasello & Call, 1997 for a review) and imitation (e.g. Itani & Nishimura 1965, 1973; Boesch 1991; Ottoni et al. 2005; Perry 2009). The subject acquiring the proper behaviour needs to observe a demonstrator and choose to perform in similar fashion when confronted to the same problem. If social learning is thought to allow techniques (and subsequently, tradition) to spread in a group, it also leads to a conformism of the answers animals choose to solve a problem (e.g. Perry 2009; Price et al. 2009).

As the set up of the experiment we performed in vervets allowed animals to gather together, it may be difficult to sort out whether the learning mechanisms are individual or social. However, we may have some insight on how quick they are leading to solving the task: allowing a low-ranking provider to open and feed from a large food resource.

METHODS

Research area, subjects and data collection

We conducted the study using two free ranging vervet monkeys groups, *Chlorocebus aethiops*, in Loskop Dam Nature Reserve in the Mpumalanga province in South Africa. The reserve is located at 180 km north/east of Pretoria and is characterised by a 'bushveld' (tall grasses and thick acacia bushes) type of habitat. It covers approximately 25000 ha, 1000 m above sea level.

The studied groups' home ranges covered about 3 km^2 and were disconnected, about three kilometres apart, one being located in a green valley (Donga group) and the other in a dry plain (Picnic group). Both groups were habituated to human observers prior to the start of the experiments. The Donga group was characterized by a fast male turn-over prior to the study period but the number of members never exceeded 15. We observed three to five adult males, seven adult females, one to two sub adult individuals and one to two infants at a time. Infant mortality was quite high as two infants out of three died during the study period.

At the same time the Picnic group showed a higher infant survival rate as five infants out of six survived during the study period. This reproductive success almost doubled the size of the group in a very short time. Thus, we observed two to three adult males, four adult females, one juvenile and two to six infants at a time. Despite these demographic changes the adult members dominance hierarchy remained stable throughout the study period (MatMan test: Donga group: $X^2_{20} = 60.67$, $p < 0.0001$, $h = 1$, $K = 1$ and Picnic group: $X^2_{23} = 48$, $p = 0.0021$, $h = 1$, $K = 1$).

Groups were followed every second day during the pre-experiment and training phases from September 2005 to the end of January 2006. Then it was followed two days in a row every four days during the experiment phase from May 2006 to the end of September 2006. The two first authors as well as four more students collected data using every ten minutes scans concentrating on the provider as well as continuous group focal samples (Altmann 1974) on all the group members. Observations were distributed throughout the day but the majority of the data

was taken from 6:00 to 13:00 and from 16:00 to 18:00 using Pendragon Forms (professional edition 4.0.00) on Palm Zire 31.

A total of 605 hours of focal samples was recorded for the ten animals of the donga group and 422 hours for the seven animals of the picnic group. Additionally we collected 170 hours of *ad libitum* observations where we recorded agonistic or social interactions between identified individuals continuously. Location, births, immigrations, disappearances and encounters were recorded on a daily basis. For the experiment, we selected the lowest-ranking females who would accept to manipulate the container as food providers, which excluded jad and aga (Donga group) and nev and isi (Picnic group) as suitable providers.

Experiment protocol

Experimental container

For the experiment, we worked with a wooden framed container (500x550x150mm; Fig.1A) kept closed by a car doors locking device (Pict.1B) with a remote control opening that we could activate when the provider would touch the lid. Thus the only action the provider had to perform to gain access to the food source was to touch the lid. We opted for such a simple food-producing action, because we were rather interested in the socio-economic effects of food production and tried to avoid that manipulative limitations of the providers could hamper their success in opening the container. The container was covered with a plastic mesh on all sides and was reinforced with a metallic grid on top. The mesh allowed the vervets to see and smell the food in the container.

A-  **B-** 

Picture 1: A- Container. B- Locking device.

Providers' training

To habituate the animals to the food container and to train the providers to operate it we conducted a training phase with 24 trials per group from October 2005 to mid-January 2006. We provided five apples per trial, each cut into 24 pieces and we opened the container by remote control as soon as the selected provider would touch it by chance. The trials were not time restricted, i.e. we waited until the providers dared to come and touch the container. During the training phase, high-ranking individuals tried to monopolise the food as soon as the container was opened, which led to serious harassment for the lower-ranking provider. In order to reduce the harassment and to positively enhance the provider into continuing to participate in the experiment, we placed two extra apples (also cut into 24 pieces) outside the container as soon as the provider opened it. This additional food supply was not necessary for the experimental phase. It took only one trial for the provider of each group to come to touch the container by chance.

Experiment

We ran the experiment phase from May to July 2006 and conducted 16 trials per group. We followed the groups until they were at a place that was suitable for the trials (open area for the container and big trees around for the vervets to rest). We then placed the container that we baited with five apples, each cut in 24 pieces. We positioned the video camera and indicated the beginning of the trial with an acoustic signal. We waited until the provider opened the container within the one hour allotted time. From that moment on, one observer continuously followed the provider for one hour while the other observers recorded the interactions of the rest of the group. We chose this one hour control as primates are thought to require about 30 minutes after a meal to have a new sensation of hunger. No extra food was provided after the opening of the container and the test was aborted if the provider did not open the container in the allotted time. This never happened for neither groups.

Data collection

During the experiment, agonistic and affiliative interactions were continuously recorded. The distances of every member of the group from the experimental container were recorded every 30 seconds. Each approach and opening of the container by the providers was video recorded with a digital video camera (Samsung VP-D361i).

Food competition test

To evaluate the rank hierarchy of the adult animals we used dry maize distributed in large patches (to prevent rough interactions) to conduct 20 food competition tests per group from September 2005 to May 2006. The tests lasted until all adult animals came to feed (from 60 to 120 minutes). For the socio-matrix we only used the recorded approach/retreat and threat/retreat unidirectional interactions.

Data Analysis

We considered all individuals ranking above the providers and who participated in the experiment as high-ranking individuals. Hence for the Donga group we considered: Sa (alpha male), Los (alpha female), Pau (2^{nd} female), bob (3^{rd} female) and Oun (4^{th} female). For the Picnic group we considered: Gai (alpha female), Ro (alpha male) and Al (2^{nd} male).

Throughout the training and experimental phases, the time required by the providers to open their container strongly dropped (Donga: from 35 minutes to less than 1 minute, Picnic: from 120 minutes to less than 10 minutes). This evolution could be explained by interconnected parameters, the most obvious being: 0- learning to open the container by touching by the provider; 1- the presence/absence of high-ranking individuals monopolising the container and 2- the occurrence of aggressive behaviours performed by these high-ranking individuals while monopolising the container. Hence, we studied each effect chronologically from trial 1 to trial 40:

we transformed each variable into temporal series using R. Statistical tests were performed using R (version 2.10.1). The alpha-level was set 0.05.

We firstly analyzed the influence of aggressiveness in general and the presence of high-ranking individuals in particular on the opening of the container by using a multiple linear regression. Secondly, we searched for inflection points (breaking points hereafter) using R. The coding considered the temporal series as curves and it defined for which points of the curve there was an inflection point. This point meant that the part of the curve prior to the breakpoint was significantly different from the part after, indicating the moment that animals behaved differently. From the breaking points we could determine the latencies required for each individual to change its behaviour. We calculated the latency of the first individuals as: $L_1 = breakpoint_1 - 0$. All remaining latencies were calculated as: $L_{i+1} = breakpoint_{i+1} - breakpoint_i$. Latencies permitted to distinguish whether all individuals learnt at the same pace.

Throughout the training and testing sessions the time required by each provider to open the container was deeply influenced by highest-ranking individuals' actions. Hence we investigate the way high-ranking individuals learned to leave the container during the trials. We compared their learning S-looking curves with theoretical ones following the formula y = min + ((max-min) / (1 + (x/S) ^P)) in which min and max respectively mean the lowest and highest values of the curve, S is the threshold of the curve and P the steepness of the slope. Concretely, S gives an indication on how fast individuals did learn anything: if S is small, then individuals learnt to leave the box in few trials. Similarly, P gives an idea of the cognitive mechanism behind the learning: if P is small, the slope is soft and tends to describe a long learning mechanism; if P is above 10, the slope is steep and describes a fast all-or-nothing learning process. We compared the theoretical and observational curves using Spearman correlations. We also transformed each dominant's

departure times into temporal series and we check for the breakpoints of each series. To verify the relevance of each individual S point, we compared it with the breakpoints.

To complete the study, we used ACF (Auto-Correlation Functions) to investigate whether consecutive trials were autocorrelated. Concretely if two trials are auto-correlated, it means that the outcome of the previous trial influences the issue of the next one. Finally, we used L-jung-Box analyses to know how many fore trials influenced the outcome of a certain trial.

RESULTS

The presence of high-ranking individuals and aggressiveness influence the opening latency

Both the time high-ranking individuals spent at less than 10m from the containers and the number of conflicts they directed at providers strongly explained the container opening time (linear regressions Donga: $R^2 = 0.825$, $F = 138.849$, dominants' departure time: $p < 0.0001$, conflicts prior to opening: $p < 0.001$; Picnic: $R^2 = 0.930$, $F = 409.283$, dominants' departure time: $p < 0.0001$, conflicts prior to opening: $p < 0.0001$).

In both groups, if we focus on the moment higher-ranking individuals left the container within at least a 10m range, this departure was significantly correlated with the elapsed time before the provider opened the container (Spearman correlations Donga: $Rho = 0.830$, $p < 0.01$; Picnic: $Rho = 0.837$, $p < 0.01$) (Fig.1).

Furthermore, at the group level, the breakpoint revealed that the temporal series could be separated in two significantly different parts. For both groups, the breakpoint was found for the trial number 10. Prior to this point, both high-ranking individuals' departure and opening times were on average significantly longer than after the point.

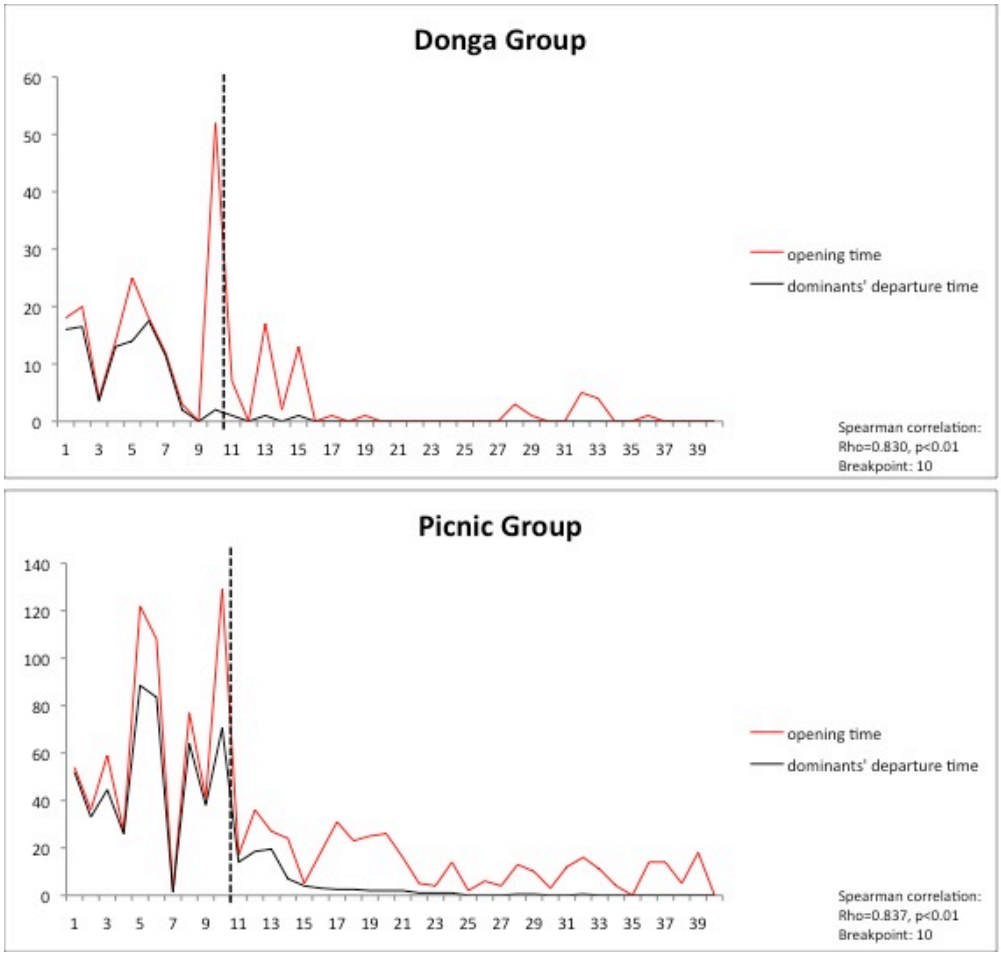


Figure 1. Plots of the moment all high-ranking individuals left the container (dominants' departure time in black) and the moment the provider opened the container (opening time in red) for the two groups. Each group breakpoint appears as a black dotted line and is set at trial number 10.

Evidences of learnt restraint at an individual level

In the Donga group two waves of learning can be identified. The alpha male Sa and female Los who first monopolised the container moved away around the second trial (S = 2.5) and hardly ever stayed next to it in the remaining trials. However, the analysis at the temporal series level showed that their active departure only became consistent around the 6th trial (breakpoint = 6).

The three next high-ranked females (Pau: beta female, Bob: 3rd female, Oun: 4th female) could then all at once approach and monopolise the container. They, in turn, learnt to move away around the seventh trial (S = 7.5, breakpoint = 8). When we compare these observed curves with

theoretical ones using a Spearman correlation the fitting is best with a slope characterised by a P > 15 (all the correlations here have been performed with a P = 20; Sa: Rho = 0.696, p < 0.01; Los: Rho = 0.697, p < 0.01; Pau: Rho = 0.686, p < 0.01; Bob: Rho = 0.771, p < 0.01; Oun: Rho = 0.740, p < 0.01; average group curve: Rho = 0.763, p < 0.01) (Fig.2).

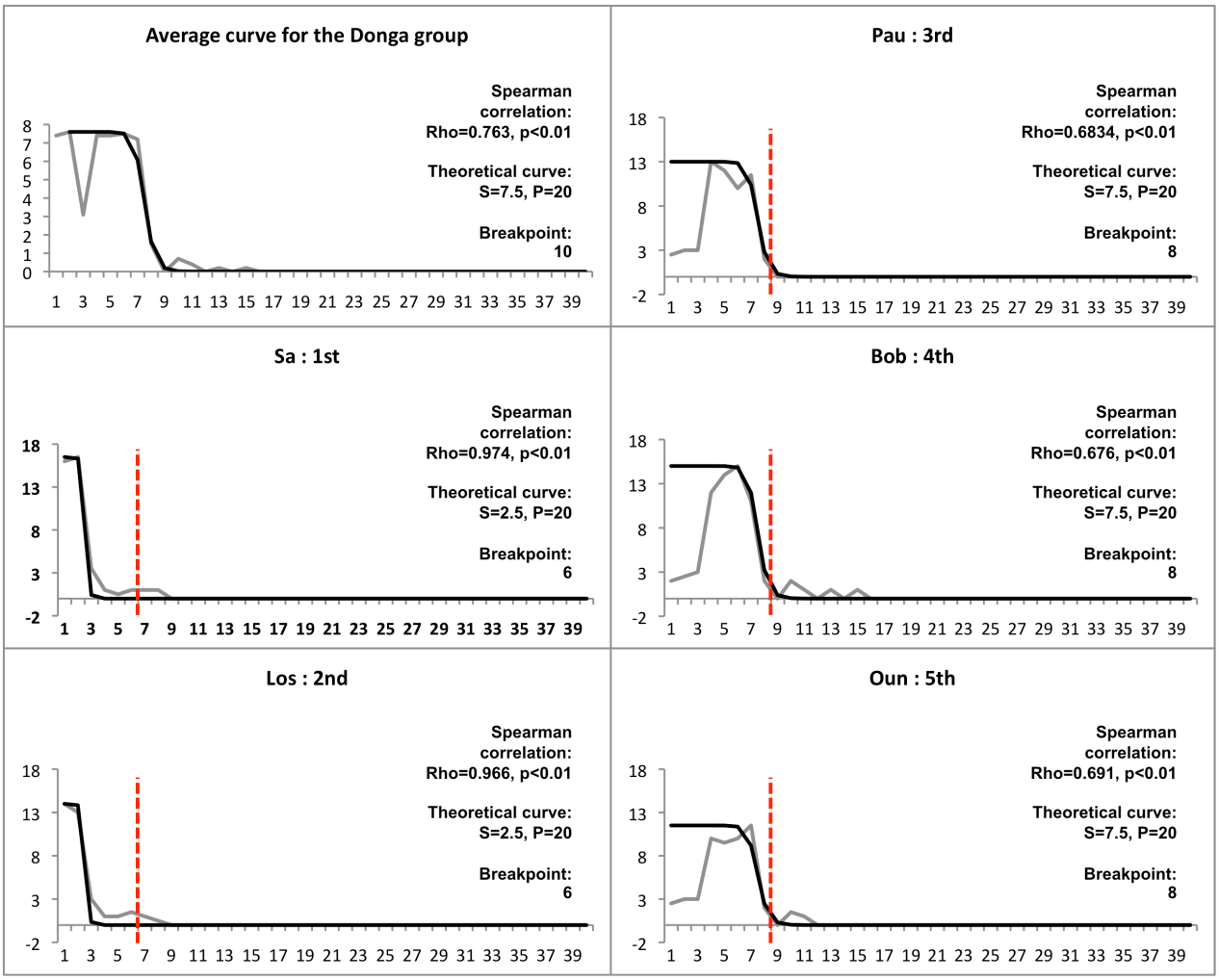


Figure 2. Donga group: Plots of the observed high-ranking individuals' departure curve (in grey) and the theoretical curve (in black). The rank of each individual is specified next to its name. Each individual breakpoint appears as a red dotted line.

When we plotted the latencies of all individuals we found that Sa and Los needed 6 trials to behave differently, while Pau, Bob and Oun only required 2 trials (Fig. 3). These three females could only learn when the effect of the two alpha individuals was removed, leading to a queuing-to-learn system. They also learnt faster than the two alpha individuals.

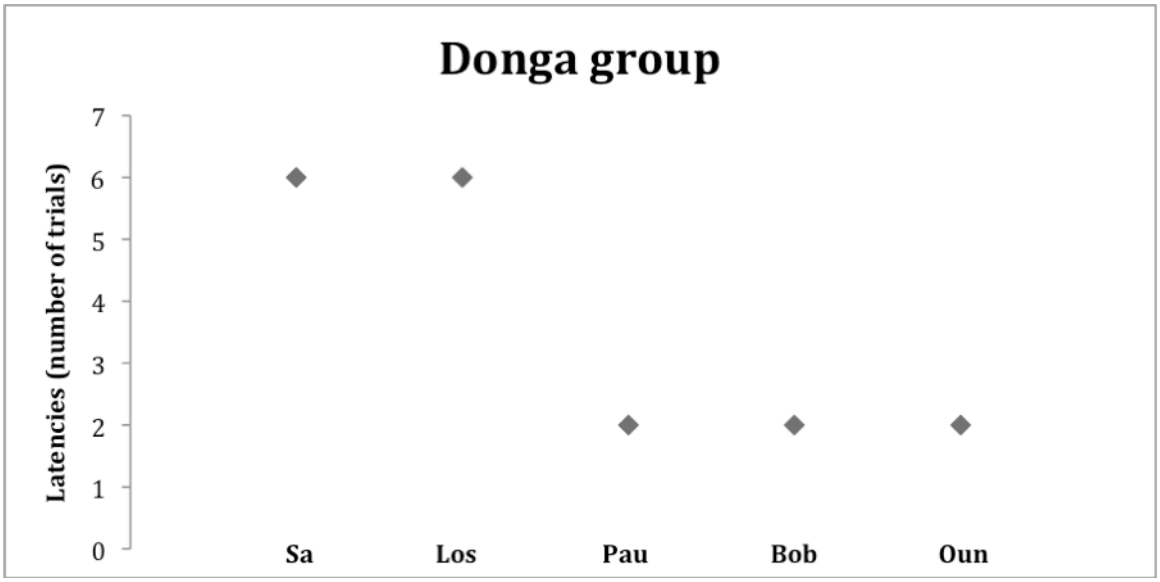


Figure 3. Latencies (number of trials) required by the high-ranking individuals to learn to leave the container after they could approach it.

We found similar effects for the Picnic group than for the Donga group: high-ranking animals learnt in turn. The alpha female Gai left the container around the sixth trial (S = 6.5, breakpoint = 7), then the alpha male left around the 10th trial (S = 10.5, breakpoint = 11) and the beta male around the 14th trial (S = 14, second breakpoint = 14). For Al, the first breakpoint (breakpoint = 7) coincides with the first trial(s) during which he could approach the container after higher-ranking Gai learned to stay away from it. When we compare these observed curves with theoretical ones using a Spearman correlation, the fitting is best for a slope defined by $P > 15$ (all the correlations were performed with a P = 20; Gai: Rho = 0.840, $p < 0.01$; Ro: Rho = 0.827, $p < 0.01$; Al: Rho = 0.694; average group curve: Rho = 0.918, $p < 0.01$) (Fig.4).

When we plotted the latencies of all individuals we found that Gai needed 7 trials to behave differently, while Ro only required 4 trials and Al 3 trials (Fig. 5), which also led to a queuing-to-learn system in which the learning speed increased from an individual to the next.

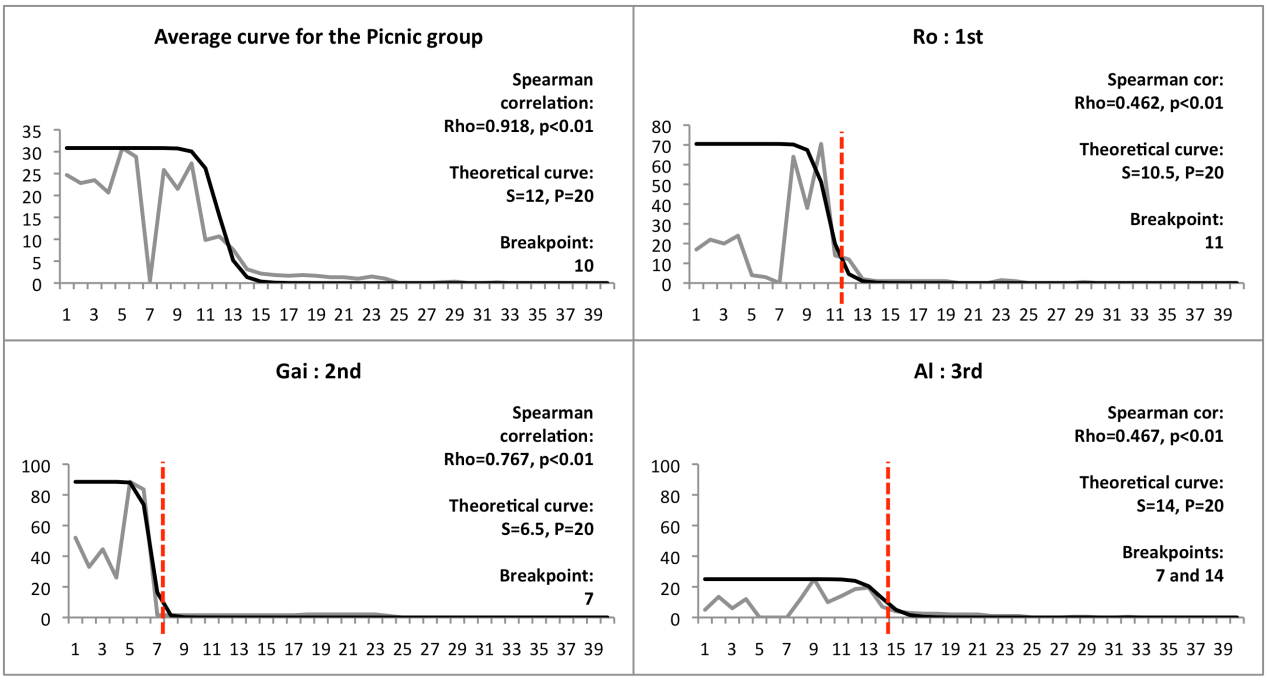


Figure 4. Picnic group: Plots of the observed high-ranking individuals' departure curve (in grey) and the theoretical curve (in black). The rank of each individual is specified next to its name. Each individual breakpoint appears as a red dotted line.

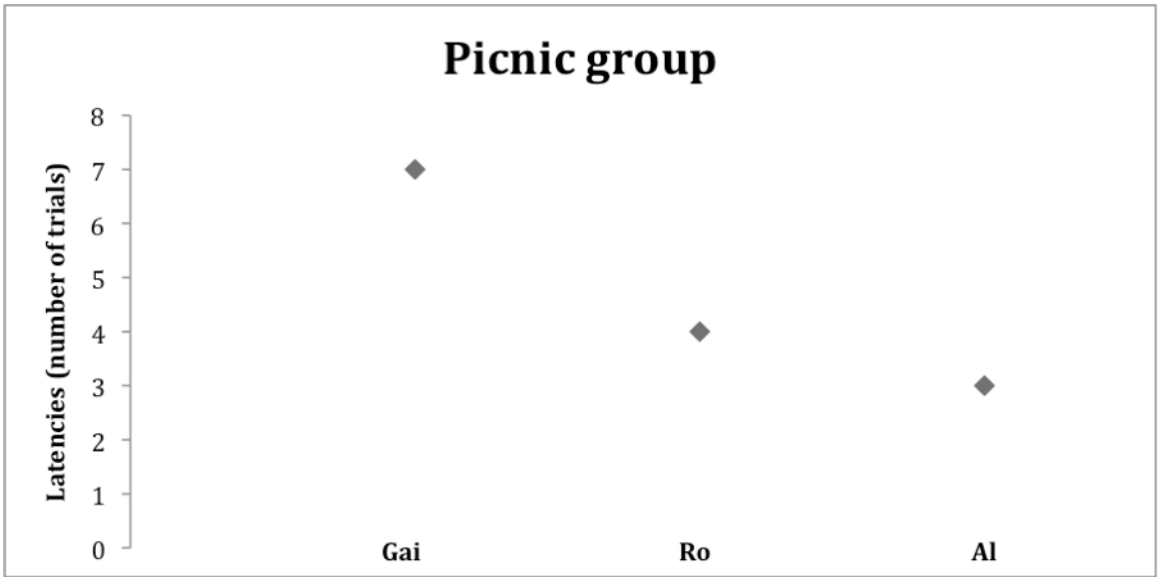


Figure 5. Latencies (number of trials) required by the high-ranking individuals to learn to leave the container after they could approach it.

Consequences of individual behaviours at the level of the group

When we considered the auto-correlation functions (ACF) of the Donga group, almost all opening times depended on the outcome of the previous trial. Conversely, dominants' departure times were random prior to the 11th trial and correlated with the previous trial afterwards. This confirmed the breaking point result we found at the group level. The number of aggressive behaviours from the high-ranking individuals also appeared to be random up to the 9th trial and auto-correlated after (Fig.6).

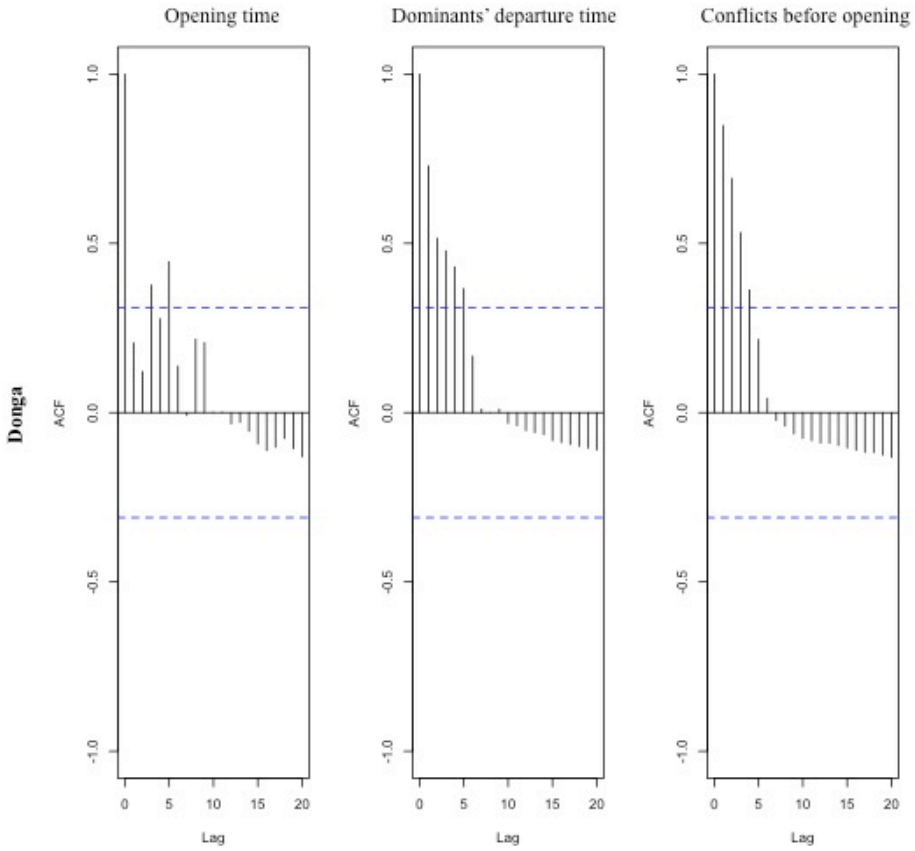


Figure 6. Plots of the autocorrelated functions for the opening time, the dominants' departure time, and the number of conflicts before the opening of the container for the Donga group. The lag between two lines represents 2 trials. Only the lines crossing the blue dotted lines held a non-significant result. All the others cannot be considered as different from 0 and mean that a trial is autocorrelated with the previous one. The first trial always has a p = 1 as it cannot be correlated with anything else than itself.

When we considered the ACFs of the Picnic group, we found similar results than for the Donga group. Almost all opening times depended on the outcome of the previous trial while dominants' departure times were random prior to the 10th trial and correlated with the previous trial afterwards. This also confirmed the breaking point result we found at the group level. The number of aggressive behaviours from the high-ranking individuals appeared to be random up to the 8th trial and correlated after (Fig.7).

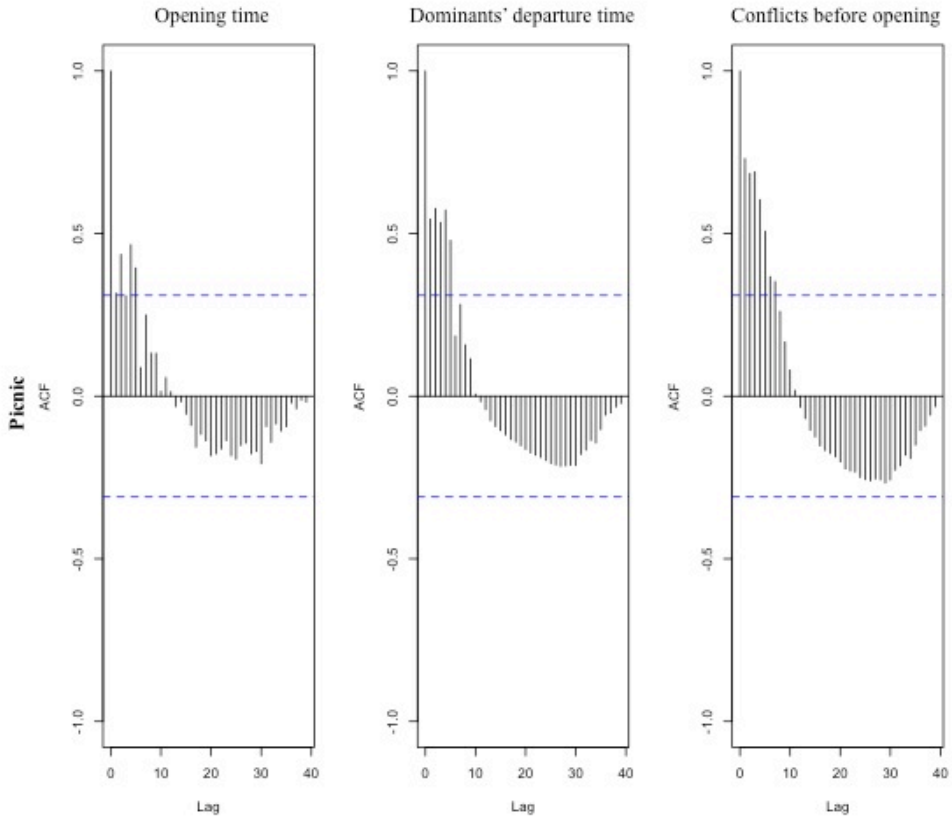


Figure 7. Plots of the autocorrelated functions for the opening time, the dominants' departure time, and the number of conflicts before the opening of the container for the Picnic group. The lag between two lines represents 1 trial. Only the lines crossing the blue dotted lines held a non-significant result. All the others cannot be considered as different from 0 and mean that a trial is autocorrelated with the previous one. The first trial always has a p = 1 as it cannot be correlated with anything else than itself.

Finally, when we considered the L-jung-Box analyses, we found that most results became significant when at least 5 previous trials could influence the outcome of a certain trial. This result held for both groups (Fig.8).

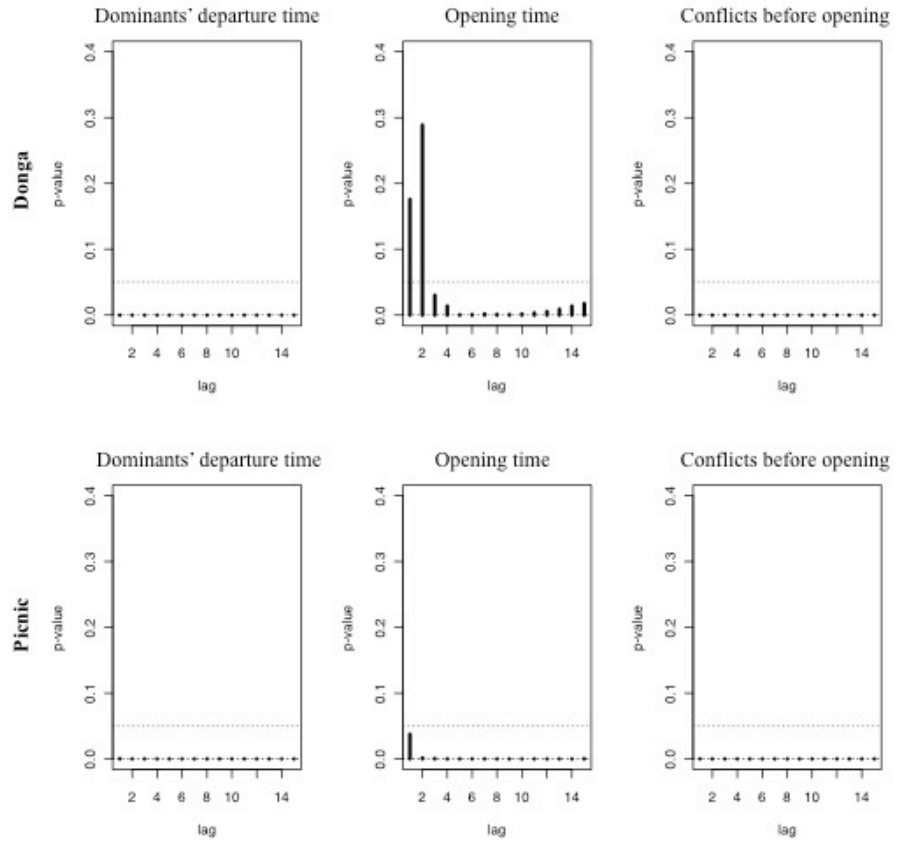


Figure 8. Plots of the L-jung-Box analyses for the dominants' departure time, the opening time, and the number of conflicts before the opening of the container. The lag between two lines represents 5 trials. Only the lines crossing the dotted line are non-significant. All the others cannot be considered as different from 0 and mean that a trial is autocorrelated with the 5 previous ones.

DISCUSSION

The emergence of self-control

In both vervet groups we found that the time required for a provider to come and open a container was seriously hampered by higher-ranking individuals' behaviours. First, at the beginning of the trials, high-ranking individuals were particularly protective over the container and aggressively targeted the providers. Contrary to results observed by Stammbach (1988) in macaques, providers would not come to open the box when dominants would linger around it. They would wait that all higher-ranking individuals reach a safe distance above 10 m from the container and preferentially that they even climbed a tree (Fig. 9). However, if some of the first trials lasted from half an hour to two hours before a provider would dare to open the container, things eased around the 10th trial as shown by the group level breaking points.

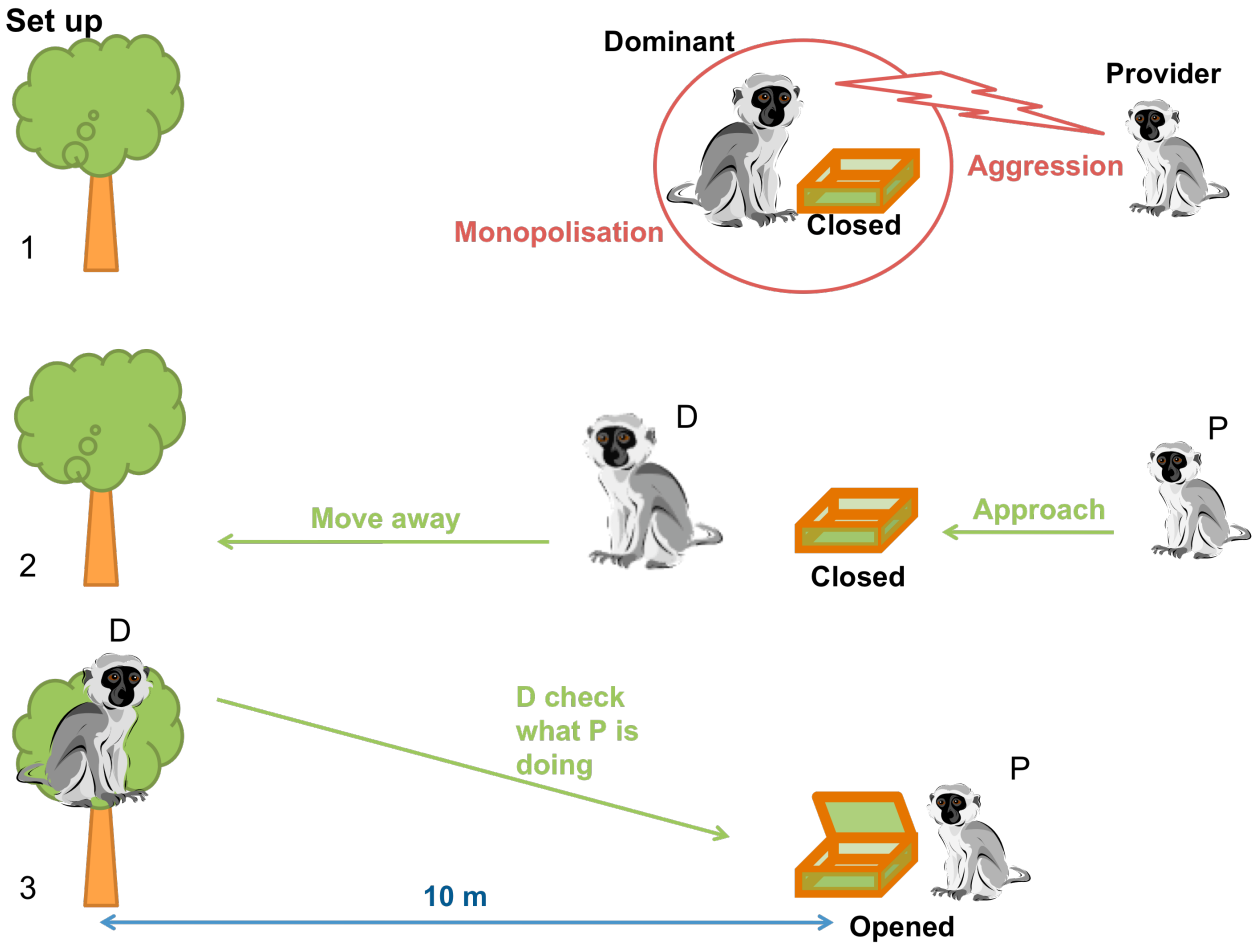


Figure 9. Summary of the animals' behaviours that are required in order to ease the opening of the container.

When we investigated the behavioural changes at an individual level, we found that all high-ranking individuals learnt to quickly and actively leave the container soon after the beginning of a trial. Indeed, the learning curves of all individuals were characterised by a steep slope ($P > 15$), which suggested a fast learning mechanism. Furthermore, in both group the learning was chronologically correlated with the rank: higher-ranked individuals first monopolized the container, then learnt to leave, then lower-ranking individuals could in turn monopolize the box, then learnt to leave and so on. For the Donga group, the learning of the last (and fifth) higher-ranking individual was matching the group breakpoint, which means that all the five individuals in turn prevented the fast opening of the container. However, for the Picnic group,

the group breaking point was related to the consecutive learning of the two first dominants only. The third individual seemed to have little impact on the provider's decision to open the container.

The fact that all individuals seemed to learn in turn and needed to experience the container monopolisation before realizing that the opening was faster if they leave, could suggests that the learning mechanisms are individual rather than socially enhanced. However, the queuing-to-learn system was coupled with a learning pace that shortened from one individual to the next. This tends to suggest that individuals did observe one another and that social emulation may have played a role in the fact that all eight high-ranking individuals chose the option to leave the container.

Learning mechanisms

In both groups we found that the opening times were hardly ever random. The ACFs results confirmed that provider's actions over the container were strongly influenced by others' aggressive behaviours and presence. However, besides these direct effects, the L-jung-Box analyses showed that a certain opening time was correlated with the five previous trials. This suggests that the provider also used the positive or negative actions she experienced during the last five trials to decide the moment she could open the container.

The ACFs also showed that high-ranking individuals' departure behaviours were random during the first trials but became autocorrelated around each group breaking point. We found a similar result for the aggressiveness, except that for the Picnic group, the aggressiveness reduction seemed to start as soon as the alpha female actively left the vicinity of the container. The randomness suggests that dominant individuals did not use a clear set of strategies but tried different approaches at each trial. However, as soon as they found an effective strategy, they used the positive outcome as an incentive to act in similar fashion during the next trial. Furthermore, the L-jung-Box analyses showed that both the high-ranking individuals' departure time and the

aggressiveness were auto-correlated up to the 5th previous trial suggesting that dominants also used previous actions to choose the appropriate behaviour.

Conclusion

The consequences of each individual bit of self-control in terms of aggressiveness reduction and monopolisation inhibition resulted in the whole group benefit, as the container and the bonanza food within were more quickly available. The fact that they would also learn in very few trials suggests that adult individuals may still have a non-negligible behavioural plasticity when they are facing natural situations in which individual benefit can be reached via social consensus, here the consensus being the temporarily access of a food resource by a low-ranking individual. The spontaneous learning to show restraint (i.e. without training by the experimenter) was achieved at the group level via a queuing-according-to-rank learning process. Individuals seemed to mainly use trial-and-error learning processes based on the outcomes they reached in the five previous trials. The learning pace however seemed to indicate that individuals also used social enhancement to learn the proper strategy. To our knowledge, this study is the first to give strong evidences of the emergence of self-control in wild conditions. It is also the first one to offer some cues as to the likely mechanisms

ACKOWLEDGEMENTS

We thank the Mpumalanga Parks Board, UNISA and ABEERU colleagues, L. Brown, L. Barrett, S. P. Henzi and R. Bshary in South Africa for research permission and logistic support. We thank S. Aubel, A. Barrett, A. Brotz, D. Carter, V. Dufour, E. Hellard, S. Lemoine for assistance in the field. We thank C. Sueur for statistical advice on the theoretical curves. NWO (Evolution and Behaviour 051-12-036) provided financial support.

CHAPTER 8

GROOMING EXCHANGES
Important parameters

Summary, discussion and conclusions

JM Fruteau

The purpose of this study was to investigate how biological market laws govern reciprocal exchanges in two primate species: sooty mangabeys and vervet monkeys. Over all the chapters we considered the factors that determine the price of commodities such as young infants or potential mates, by largely investigating quantitative aspects rather than qualitative ones. We find that as human markets, primate markets are characterized by fluctuating exchange rates depending essentially on supply and demand ratios (Noë & Hammerstein 1994, 1995). Along with the law of supply and demand, we have investigated the effects of power asymmetries between partners and, in some cases, outbidding competition.

Trading classes' identification and reciprocal grooming exchanges

In both mangabeys and vervets, we calculate that adult females spend about 15% of their daily budget to grooming, which represents around three to four hours of grooming per day. In the meantime, an average grooming session length is above five minutes, which means that females can have plenty of time to interact with as many partners as they see fit. However, and even in small groups like vervets, most females interacts with two to four preferred partners with which they spend a disproportional amount of their grooming time. Frequent partners groom each other for at least 10 min per day while on average, infrequent partners groom each other for less than 10 min a month in mangabeys and less than 10 min a week in vervets. In females of adjacent ranks and outside any reproductive periods, grooming seems to be only given for grooming and no other commodity. Closely ranked females generally tend to give as much grooming as they get. While we do not have the genetic relatedness of the mangabey females, we find that in the Donga group, vervet females of adjacent rank belongs to the same matriline, while in the Picnic group, none of the females are affiliated. In the Donga group however, affiliation does not predict whether females are frequent or infrequent groomers.

For decades, many studies have reduced the complexity of the multiple factors prevailing in exchanges between individuals (and on a larger scale in cooperation) into simple repeated

dyadic interactions allowing partner control strategies (e.g. Axelrod 1980; Axelrod & Hamilton 1981; Dugatkin & Wilson 1991; Enquist & Leimar 1993). In both our study species, most grooming sessions can be described as a succession of bouts during which the two partners groom each other in turn. This dyadic structure seems a perfect setting to investigate some of the partner control strategies such as parceling (Connors 1995) or raising the stakes (Roberts & Sherratt 1998), but females fail to use any. Our results show that females invest in longer bouts at the beginning of the sessions, which is in contradiction to exploitation prevention (parcelling strategy) or trust building (raising the stake strategy). Some authors (Colmenares et al. 2002; Schino et al. 2003; see also Gumert 2007b) emphasized that the difficulty to clearly identify trading classes can lead to erroneously reject market mechanisms. In grooming for grooming exchanges, there are typically two kinds of situations. In the first, females are of adjacent rank (and usually frequent groomers) and their exchanges are expected to remain more or less symmetric. In the second, females are not of adjacent rank (and usually infrequent groomers) and their exchanges are expected to be biased toward the individual that cannot offer anything else but grooming (usually, the lower-ranking partner). Hence assuming that the dichotomy frequent/infrequent partners is relevant for our study species, we compared the grooming sessions occurring in both cases. Interestingly, we find that infrequent groomers do not build trust. The first bout they give at the beginning of a session cannot predict the length of the session. In contrast, the first invested bout in frequent groomers predicts the length of the session. Its length is directly correlated to the length of the rest of the grooming session, long first bouts predicting long sessions. While this finding does not directly demonstrate trust building, it still suggests that females have a good knowledge of the quality of their relationships with others. It also gives some evidences for the biological market main control mechanism: switching partners. Indeed, the “playing off partners” predicts that animals base their preferences on past experiences with multiple partners. These experiences reach back deeper in the past than either parcelling or raising the stakes (e.g. de Wall

2000, Fruteau et al. 2009, Schino & Pellegrini 2009). This very first bout seems to give both partners an indication of the quality of the interaction that follows.

Grooming secures the cooperative state of the partner

While it proved difficult to define the trading classes in grooming-grooming exchanges, no such problem plagued grooming-infant handling exchanges. In this case, we distinguish easily between non-mother and mother of less than three months old infants. The former gives all the grooming while the latter hardly reciprocates and rather grants access to her infant. We find that females highly value infants as they give longer grooming bouts to be able to handle them rather than to receive reciprocated grooming. We also find that the interactions between mothers and handlers are incredibly complex and multi-layered. The amount of grooming non-mothers gives to get access to infants is influenced by the infants' availability, their age and the rank distance existing between the handler and the mother. The length of grooming provided varies sufficiently to reflect many small changes such as the infants growing older. It also shows that females are able to adjust their grooming behaviours constantly. Interestingly, grooming bouts seem to secure the cooperative state of the mothers: they do not easily give access to their infants but tolerate handling as soon as they receive the necessary amount of grooming.

We find similar results when we study the grooming-sex interactions in mangabeys. The sex market is one of the oldest paradigms demonstrating the impact of competition on the selection of particular sexual traits and behaviours (see Andersonn 1994 for an extensive review). Accessing a mate and reproducing are two of the main drives directing adult animals lives, and primates do not make exception. Hence it is interesting to know that a low-cost action like grooming can secure sexual activities. In sooty mangabeys, males and females sexual roles are not as classical as in other primate species. Indeed, females appear to be the most active gender seeking for sexual opportunities. Besides repeatedly presenting their sexual parts to males, receptive females use grooming as a strategy to promote mating. In cases where males initially are

not eager to engage in any sexual activities when females do not display maximum tumescence, they change their mind when grooming is part of the foreplay. We observe that females also differentiate between 1) resident and immigrant males by initiating grooming-sex interactions more often with the latter, and between 2) high-ranking and low-ranking males by grooming the former after the mount and the latter before the mount. Females' different behaviours towards males can be explained by the different nature of their relationships. We demonstrate that females and resident males actively cooperate to reduce infanticidal risks (Fruteau et al. 2010) and that females may use grooming to keep the bond with these males intact. In the case of immigrant or low-ranking males however, receptive females would initiate grooming sessions in exchange for multi-male mating (MMM: Wolff & Macdonald 2004) since MMM is thought to enhance paternity confusion and thereby deter infanticide risks. Furthermore, the MMM hypothesis would also explain for the moment receptive females choose to groom males. In fact, females give loud copulation calls directly after the mount, which attracts other males. We observe that higher-ranking males then replace the previous male and mate with the female. Hence, grooming low-ranking males after a mount in order to secure sex opportunities would simply not work.

A partner's intrinsic value and the law of supply and demand

Natural occurrences

In all studies we find that grooming investments are affected by the rank difference existing between two partners. In grooming-grooming interactions and for both species, the subordinate female of a dyad has to groom her partner longer than she is groomed in return. Similarly, in grooming-infant handling exchanges, higher-ranking females groom mothers a lot less than do lower-ranking females in order to get access to the infant. This difference of leverage between females has been explained by the fact that dominants may have additional commodities (tolerance at food patches, restraint in dyadic conflicts with the subordinate, agonistic support in conflicts) to trade that subordinates cannot offer. The number of available infants per female has a

strong effect on handler's grooming investments. When infants are rare, grooming bouts are longer. Similarly, non-mothers invest in longer bouts when infants are younger. These findings suggest that grooming-infant exchanges follow the market law of supply and demand: the value of infants varies through time according to their maturity and their fluctuating availability affects the outbidding competition among handlers who adapt their grooming investments accordingly.

In mangabeys, we show that during the mating period, females vary their grooming investment according to their receptive status. This contrasts with previous results found in longtailed macaques in which swelling stages did not affect the way males valued females (Gumert 2007b). In mangabeys however, females exchange grooming for mating when they are receptive and they groom males significantly longer when they are at the first stages of their sexual cycles. When they display maximum tumescence and are therefore close to ovulation, their grooming investments decrease noticeably. This suggests that females are conscious of their intrinsic value. Since males still mates with them despite the smaller amount of grooming they receive, they seem to acknowledge females' higher receptive value.

We observe that the number of males present and females simultaneously receptive often fluctuate throughout the mating period: the ratio available males per receptive females varies from day to day. We show that receptive females groom males longer when there are fewer available males in the group. This suggests that grooming-for-sex exchanges follow the market law of supply and demand: the value of females varies through time according to their sexual receptivity and males' fluctuating availability affects the outbidding competition among these receptive females in terms of grooming duration. Hence the conclusions we draw from the sexual market hold many similarities with the conclusions for the infant market: females as well as males seem to accurately evaluate their immediate and fluctuating social environment and choose the amount of investment accordingly.

Testing the predictions derived from the law of supply and demand in vervets

In vervets we performed the first field-experiment to investigate the law of supply and demand under more controlled conditions. We created an artificial market in our two study groups and caused sudden changes in the market value of two low-ranking females in such a way that these affected all other group members and could easily be perceived by them. In a first step, we allowed, in each group, a single female to produce a bonanza of food for her and the rest of the group by triggering the opening of a container. In a second step, we introduced, in each of these groups, a second provider with a second food container that only she could open. The two boxes were made available simultaneously, but were not necessarily opened simultaneously. In economic terms we replaced a monopoly by a duopoly. We expected that if primates understand naturally occurring trades, their knowledge would be a sufficiently inherent part of their behavioural repertoire to be adapted to a completely new – and rather artificial - situation. In the first step, we find that grooming ratios shift to the advantage of the food providers, which is similar with the results of Stammbach (1988) study on captive long-tailed macaques. Our crucial result in terms of biological market expectations however, occurs during the second step when the positive effect on the grooming ratios of the first providers is roughly half as strong after we added the second provider. This gives strong evidence that primates are able to deal with supply and demand ratios accurately and rapidly.

Proximate mechanisms allowing exchanges

The experiment that we performed in vervets raised several questions on the necessary mechanisms allowing the performance of the market. The first one is motivated by the fact that group members are eager to exchange grooming for something they can have for free whenever they wait long enough: why do they not simply wait? Our explanation is that while large amount of food holds more value than a simple grooming-grooming interaction, this value decreases with

time. In other words, our conclusion is that vervets, like many other animals, discount future benefits and value a reward more the sooner it becomes available (Stevens & Stephens 2008).

During the training phase of the experiment, we also realized that the providers were reluctant to open the container in the presence of high-ranking animals. Indeed, in both groups, high-ranking individuals were particularly protective over the container and aggressively targeted the providers, hampering with the opening of the box. Contrary to results observed by Stammbach (1988), providers did not come to open the box when dominants lingered around it. They rather waited until these have left and were at a safe distance form the box (> 10m). Some of the first trials lasted from half an hour to two hours before a provider opened the box. However, all high-ranking individuals learnt to quickly and actively leave the vicinity of the container soon after the beginning of a trial. All individuals learnt in turn, the higher-ranking individuals learning first. In other words, each individual needed to experience the container monopolisation before realizing that the opening was faster when it left. We conclude that the inhibition of the monopolisation is due to trial-and-error learning mechanisms. However, the consequences of each individual bit of self-control in terms of aggressiveness reduction and monopolisation inhibition resulted in the whole group benefit, as the container and the food within were more quickly available.

The quick emergence of such self-control over the whole population of high-ranking individuals also suggests that adult individuals still have a non-negligible behavioural plasticity. Many studies involving the emergence of elaborating foraging techniques using objects or tools often argued that adult individuals are less effective at acquiring a new technique than young individuals (e.g. Kawai 1965, Byrne & Suomi 1996). Our results suggest that when adult individuals are facing situations in which individual benefit could be reached via social consensus (here, the momentarily allowance of the access of a food resource by a subordinate), the outcomes are altogether different. Individuals understand the situation quickly and do not need many repetitions to adapt their behaviours. Actually, we find that during the first trials, individuals do not use a clear set of strategies but try different approaches. However, as soon as they find an

effective strategy, they use the positive outcome as an incentive to act in similar fashion during the next trial.

Conclusion

In conclusion, the adjustment of grooming investment can be understood as a process in which each individual's offers depend on its perception of the other's value as a partner. Indeed, during a grooming session both partners can test their momentary market value by ending a grooming bout and monitoring their partner's reaction. Grooming plays a dual role in this process: it functions both as a currency, because of its direct influence on the reward system of the groomed partner and as a commodity, because it can be traded directly for access to infants, sex and so forth. Grooming can thus be used to balance asymmetries in trades of other commodities. In our natural infant and sex markets as well as in our experiment this balance can shift suddenly. Grooming patterns are however quickly adjusted. Thus, free ranging monkeys can accurately adjust to changing market conditions, although they cannot rely on language for bargaining and have no obvious way of concluding binding contracts.

REFERENCES

Adam, T. C. 2010. Competition encourages cooperation: client fish receive higher-quality service when cleaner fish compete. *Animal Behaviour*, 79, 1183-1189.

Alberts, S.C. 1999. Paternal kin discrimination in wild baboons. *Proceedings of Royal Society B*., 206, 1501-1506.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, 2504, 227-265.

Altmann, J. 1980. *Baboon mothers and infants*. Cambridge, Massachusetts: Harvard University Press.

Anderson, J.R., Awazu, S. & Fujita, K. 2000. Can squirrel monkeys (*Saimiri sciureus*) learn self-control? A study using food array selection tests and reverse-reward contingency. *Journal of Experimental Psychology: Animal Behavior Processes*, 26, 87-97.

Andersson, M. 1994. *Sexual selection*. Princeton, New Jersey: Princeton University Press.

Angst, W. & Thommen, D. 1977. New data and a discussion of infant killing in old world monkeys and apes. *Folia Primatologica*, 27, 198-229.

Axelrod, R. 1980. Effective choice in the prisoner's dilemma. *Journal of Conflict Resolution*, 24, 3-25.

Axelrod, A. & Hamilton, W.D. 1981. The evolution of cooperation. *Science*, 211, 1390-1396.

Axèn, A.H. 2000. Variation in behavior of lycaenid larvae when attended by different ant species. *Evolutionary Ecology*, 14, 611-625.

Baillet, D. 2010. Communication and cooperation in social dilemmas: a meta-analytic review. *Journal of Conflict Resolution*, 54 (1), 39-57.

Barnard C.J. & Sibly R.M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour*, 29, 543-550.

Barrett, L. & Henzi, S. P. 2001. The utility of grooming in baboon troups. In *Economics in nature: social dilemmas, mate choice and biological markets*. (ed. by R. Noë, J.A.R.A.M. van Hoof & P. Hammerstein), pp 119-145, Cambridge University Press, Cambridge.

Barrett, L. & Henzi, S. P. 2006. Monkeys, markets and minds: biological markets and primate sociality. In *Cooperation in Primates and Humans: Mechanisms and Evolution* (ed. by P.M. Kappeler & C.P. van Schaik), pp. 209-232, Berlin, Springer.

Barrett, L., Gaynor, D. & Henzi, S. P. 2002. A dynamic interaction between aggression and grooming reciprocity among female chacma baboons. *Animal Behaviour*, 63, 1047-1053.

Barrett, L., Henzi, S.P. & Dunbar, R.I.M. 2003. Primate cognition: from `what now?' to `what if ?' *TICS,* 7, 494-497.

Barrett, L., Henzi, P., Weingrill, T., Lycett, J.E. & Hill, R.A. 1999. Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B.*, 266, 665-670.

Barrett, L., Henzi, P., Weingrill, T., Lycett, J.E. & Hill, R.A. 2000. Female baboons do not raise the stakes but they give as good as they get. *Animal. Behaviour*., 59, 763-770.

Barton, R. 1985. Grooming site preferences in primates and their functional implications. *International Journal of Primatology*, 6, 519-532.

Batali, J. & Kitcher, P. 1995. Evolution of altruism in optional and compulsory games. *Journal of Theoretical Biology,* 175,161-171.

Baumgartner, T., Heinrichs, M., Vonlanthen, A., Fischbacher, U. & Fehr, E. 2008. Oxytocin Shapes the Neural Circuitry of Trust and Trust Adaptation in Humans. *Neuron,* 58, 639-650.

Bercovitch, F.B. 1988. Coalitions, cooperation and reproductive tactics among adult male baboons. *Animal Behaviour*, 36, 1198-1209.

Bergmüller, R., Johnstone, R.A., Russell, A.F. & Bshary, R. 2007. Integrating cooperative breeding into theoretical concepts of cooperation. *Behavioural Processes*, 76, 61-72.

Bertram, B.C.R. 1978. Living in group: predators and prey. In: *Behavioural Ecology: an evolutionary approach* (ed by J.R. Krebs and N.B. Davies). First edition. pp: 64-96. Oxford: Blackwell Scientific Publications.

di Bitetti, M.S. & Janson, C.H. 2001. Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. *Animal Behaviour*, 62, 47-56.

Boesch, C. 1991. Teaching among wild primates. *Animal Behaviour*, 41, 530-532.

Boggess, J. 1984. Infant killing and male reproductive strategies in langurs (*Presbytis entellus*). In: *Infanticide: Comparative and Evolutionary Perspectives* (ed. by G. Hausfater and S.B. Hrdy). pp: 283-310. New York: Aldine de Gruyter.

Borries, C. 1992. Grooming site preferences in female langurs (Presbytis entellus). *International Journal of Primatology*, 13, 19-32.

Borries, C. 1997. Infanticide is seasonally breeding multimale groups of Hanuman langurs (*Presbytis entellus*) in Ramnagar (South Nepal). *Behavioural and Ecological Sociobiology*, 41, 139-150.

Borries, C., Launhardt, K., Epplen, C., Epplen, J.T. & Winkler, P. 1999a. DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys. *Proceedings of the Royal Society B.,* 266, 901-904.

Borries, C., Launhardt, K., Epplen, C., Epplen, J.T. & Winkler, P. 1999b. Male as infant protectors in Hanuman langurs (*Presbytis entellus*) living in multi-male groups – defense pattern, paternity and sexual behaviour. *Behavioural and Ecological Sociobiology*, 46, 350-356.

Boysen, S.T. & Berntson, G.G. 1995. Responses to quantity: perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes*, 21, 82-86.

Boysen, S.T., Berntson, G.G., Hannan, M.B. & Cacioppo, J.T. 1996. Quantity-based interference and symbolic representations in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes*, 22, 76-86.

Brakefield, P. M. 1987. Industrial melanism: Do we have the answers? *Trends in Ecology & Evolution*, 2, 117-122.

Bronstein, J. L. 1998. The contribution of ant plant-protection studies to our understanding of mutualism. *Biotropica*, 30, 150-161.

Broom, M., Borries, C. & Koenig, A. 2004. Infanticide and infant defence by males -- modelling the conditions in primate multi-male groups. *Journal of Theoretical Biology*, 231, 261-270.

Brosnan, S., Silk, J., Henrich, J., Mareno, M., Lambeth, S. & Schapiro, S. 2009. Chimpanzees *(Pan troglodytes)* do not develop contingent reciprocity in an experimental task. *Animal Cognition*, 12, 587-597.

Bshary, R. 2001. The cleaner fish market. In *Economics in nature: social dilemmas, mate choice and biological markets*. (ed. by R. Noë, J.A.R.A.M. van Hoof & P. Hammerstein), pp 146-172, Cambridge University Press, Cambridge.

Bshary, R. 2002. Building up relationships in asymmetric co-operation games between the cleaner wrasse *Labroides dimidiatus* and client reef fish. *Behavioural Ecology and Sociobiology*, 52, 365-371.

Bshary, R. & Bronstein, J.L. 2004. Game structures in mutualistic interactions: what can the evidence tell us about the kind of model we need? *Advances in the Study of Behavior*, 59-101.

Bshary, R. & Grutter, A.S. 2002a. Experimental evidence that partner choice is a driving force in the payoff distribution among cooperators and mutualists: the cleaner fish case. *Ecology Letters*, 5, 130-136.

Bshary, R. & Grutter, A.S. 2002b. Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Animal Behaviour*, 63, 547-555.

Bshary, R. & Grutter, A.S. 2006. Image scoring and cooperation in a cleaner fish mutualism. *Nature*, 441, 975-978.

Bshary, R. & Noë, R. 2003. Biological markets – The ubiquitous influence of partner choice on the dynamics of cleaner fish – client reef fish interactions. In: *Genetic and cultural evolution of cooperation*. (ed. by P. Hammerstein), pp 167-184, the MIT Press, Cambridge, Massachussetts.

Bshary, R., Grutter, A.S., Willener, A.S.T. & Leimar, 0. 2008. Pairs of cooperative cleaner fish provide better service quality than singletons. *Nature*, 455, 964-967.

Buchan, J. C., Alberts, S. C., Silk, J. B. & Altmann, J. 2003. True paternal care in a multi-male primate society. *Nature*, 425, 179-181.

Bull, J. J. & Rice, W. R. 1991. Distinguishing mechanisms for the evolution of cooperation. *Journal of Theoretical Biology,* 149, 63-74.

Busse, C. & Gordon, T.P. 1983. Attacks on neonates by a male mangabey (*Cercocebus atys*). *American Journal of Primatology*, 5, 345-356.

Byrne, R.W. 2000. How monkeys find their way: leadership, coordination and cognitive maps of African baboons. In: *On the Move. How and Why Animals Travel in Groups.* (ed. by S. Boinski & P. Garber), Chicago University Press, pp 491-518.

Byrne, G. & Suomi, S.J. 1996. Individual differences in object manipulation in a colony of tufted capuchins. *Journal of Human Evolution*, 31, 259-267.

Caine, N.G., Addington, R.L. & Windfelder, T.L. 1995. Factors affecting the rates of food calls given by red-bellied tamarins. *Animal Behaviour,* 50, 53-60.

Chancellor, R.L. & Isbell, L.A. 2009. Female grooming markets in a population of gray-cheeked mangabeys (Lophocebus albigena). *Behavioral Ecology*, 20, 79-86.

Chapman, C.A. & Lefebvre, L. 1990. Manipulating foraging group size: spider monkey food calls at fruiting trees. *Animal Behaviour,* 39, 891-896.

Chapuis, L. & Bshary, R. 2010. Signalling by the cleaner shrimp Periclimenes longicarpus. *Animal Behaviour*, 79, 645-647.

Chiang, Y.-S. 2010. Self-interested partner selection can lead to the emergence of fairness. *Evolution and Human Behavior*, 31, 265-270.

Clarke, M. R., Glander, K. E. & Zucker, E. L. 1998. Infant-nonmother interactions of free-ranging mantled howling monkeys (Alouatta palliata) in Costa Rica. *International Journal of Primatology*, 1, 451-472.

Clements, K.C. & Stephens, D.W. 1995. Testing models of non-kin cooperation: mutualism and the Prisoner's Dilemma. *Animal Behaviour*, 50, 527-535.

Clutton-Brock, T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, 296, 69-72.

Clutton-Brock, T.H. & Parker, G.A. 1995. Sexual coercion in animal societies. *Animal Behaviour*, 49, 1345-1365.

Clutton-Brock, T.H. & Vincent, A.C.J. 1991. Sexual selection and the potential reproductive rates of males and females. *Nature*, 351, 58-60.

Collins, D.A., Busse, C.D. & Goodall, J. 1984. Infanticide in two populations of savanna baboons. In: *Infanticide: Comparative and Evolutionary Perspectives*. (ed. by G. Hausfater and S.B. Hrdy). pp: 193-215. New York: Aldine de Gruyter.

Collishaw, G & Dunbar, R.I.M. 1991. Dominance rank and mating success in male primates. *Animal Behaviour*, 41, 1045-1056.

Colmenares, F., Zaragoza, F. & Hernàndez-Lloreda, M.V. 2002. Grooming and coercion in one-male units of hamadryas baboons: market forces or relationship constraints? *Behaviour*, 139, 1525-1553.

Connor, R.C. 1992. Egg-trading in simultaneous hermaphrodites: an alternative to Tit-for-Tat. *Journal of Evolutionary Biology*, 5, 523-528.

Connor, R.C. 1995. Impala allogrooming and the parcelling model of reciprocity. *Animal Behaviour*, 49, 528-530.

Curio, E. 1988. Cultural transmission of enemy recognition in birds. In: *Social learning psychological and biological perspectives*. (ed. by Zentall, T.R. & Galef, B.G.). Hillsdale, NJ: Lawrence Erlbaum Inc. pp. 75-78.

Denison, R.F., Bledsoe, C., Kahn, M., O'Gara, F., Simms, E.L. & Thomashow, L.S. 2003, Cooperation in the rhizosphere and the 'free rider' problem. *Ecology*, 84, 838-845.

Deputte, B.L. 1991. Reproductive parameters of captive grey-cheeked mangabeys. *Folia Primatologica*, 57, 57-69.

Dittus, W.P. 1984. Toque macaque food calls: semantic communication concerning food distribution in the environment. *Animal Behaviour,* 32, 470-477.

Dolhinow, P. 1977. Normal Monkeys? *American Scientist*, 65, 266.

Donaldson, Z.R., Young, L.J. 2008. Oxytocin, Vasopressin, and the Neurogenetics of Sociality. *Science,* 322, 900-904.

Dufour, V., Sterck, E.H.M., Pelé, M. & Thierry, B. 2007. Chimpanzee (*Pan troglodytes*) anticipation of food return: coping with waiting time in an exchange task. *Journal of Comparative Psychology*, 121, 145-155.

Dugatkin, L.A. 1997. *Cooperation among animals: an evolutionary perspective*. Oxford University Press.

Dugatkin, L.A. & Wilson, D.S. 1991. ROVER: a strategy for exploiting cooperators in a patchy environment. *American Naturalist*, 138, 687-701.

Dunbar, R. I. M. 1988. *Primates social systems*. Chapman & Hall, London.

Dunbar, R. I. M. & Dunbar, P. 1988 Maternal time budgets of gelada baboons. *Animal Behaviour*, 970-980.

Dunbar, R. I. M. 1991. Functional significance of social grooming in primates. *Folia primatologica*, 57, 121-131.

Dunbar, R. I. M. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*, 31, 35-49.

Dunbar, R.I.M. 2008. The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. *Neuroscience Biobehaviour Reviews,* in press.

Edwards, D. P., Hassall, M., Sutherland, W. J. & Yu, D. W. 2006. Selection for protection in an ant–plant mutualism: host sanctions, host modularity, and the principal–agent game. *Proceedings of the Royal Society B-Biological Sciences*, 273, 595 - 602.

Efron, B. 1982. The jackknife, the bootstrap, and the resampling plans. Society of Industrial and Applied Mathematics, Philadelphia.

Elgar, M.A. 1986. House sparrows establish foraging flocks by giving chirrup calls if resources are divisible. *Animal Behaviour,* 34, 169-174.

Emlen, S.T. & Oring, L.W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science*, 197, 215-223.

Enquist, M. & Leimar, O. 1993. The evolution of cooperation in mobile organisms. *Animal Behaviour*, 45, 747-757.

Epstein, R., Kirshnit, C.E., Lanza, R.P. & Rubin, R.C. 1984. "Insight" in the pigeon: antecedents and determinants of an intelligent performance. *Nature*, 308, 61-62.

Fairbanks, L.A. 1990. Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour*, 9, 425-441.

Fairbanks, L.A. & Mc Guire, M.T. 1987. Mother-infant relationships in vervet monkeys: response to new adult males. *International Journal of Primatology*, 8, 351-366.

Fashing, P. J. 2001. Male and female strategies during intergroup encounters in guerezas *(Colobus guereza)*: evidence for resource defense mediated through males and a comparison with other primates. *Behavioral Ecology and Sociobiology*, 50, 219-230.

Fleming, T.H. & Holland, J.N. 1998. The evolution of obligate pollination mutualisms: senita cactus and senita moth. *Oecologica*, 114, 368-375.

Frank, R.E. & Silk, J.B. 2009. Grooming exchange between mothers and non-mothers: the price of natal attraction in wild baboons (*Papio anubis*). *Behaviour*, 146, 889-906.

Friedman, J. W. & Hammerstein, P. 1991. To trade, or not to trade; that is the question. In: *Game equilibrium models I*. (Ed. by R. Selten). Berlin: Springer.

Fruteau, C., Range, F. & Noë, R. 2010. Infanticide risk and infant defence in multi-male free-ranging Sooty Mangabeys, Cercocebus atys. *Behavioural Processes*, 83, 113-118.

Fruteau, C., Voelkl, B., vanDamme, E. & Noë R. 2009. Supply and demand determine the market value of food providers in wild vervet monkeys. *PNAS*, 106, 12007-12012.

Garber, P.A. 1997. One for all and breeding for one: cooperation and competition as a tamarind reproductive strategy. *Evolutionary Anthropology*, 5, 187-199.

Genty, E., Palmier, C. & Roeder, J.J. 2004. Learning to suppress responses to the larger of two rewards in two species of lemurs, *Eulemur fulvus* and *Eulemur macaco*. *Animal Behaviour*, 67, 925-932.

Gilby, I. C., Emery Thompson, M., Ruane, J. D. & Wrangham, R. 2010. No evidence of short-term exchange of meat for sex among chimpanzees. *Journal of Human Evolution*, In Press.

Ginther, A. J. & Snowdon, C. T. 2009. Expectant parents groom adult sons according to previous alloparenting in a biparental cooperatively breeding primate. *Animal Behaviour*, 78, 287-297.

Goldizen, A.W. 1987. Tamarins and marmosets: Communal care of offspring. In: *Primate Societies* (Ed. By B.B. Smutts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker), pp. 34-43. Chicago: University of Chicago Press.

Gomes, C. M. & Boesch, C. 2009. Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS ONE*, 4, e5116.

Goodall, J. 1986. *The chimpanzees of Gombe*. Cambridge, MA: Harvard University Press.

Gordon, T.P., Gust, D.A., Busse, C.D. & Wilson, M.E. 1991. Hormones and sexual behavior associated with post conception perineal swelling in the sooty mangabey (*Cercocebus torquatus atys*). *International Journal of Primatology*, 12, 585-597.

Greene, E, Lyon, B.E., Muehter, V.R., Ratcliffe, L, Oliver, S.J. & Boag, P.T. 2000. Disruptive sexual selection for plumage coloration in a passerine bird. *Nature*, 407, 1000-1003.

Groves, C.P. 1978. Phylogenetic and population systematics of the Mangabeys (primates: *Cercopithecoidea*). *Primates*, 19, 1-34.

Gubry-Rangin, C., Garcia, M. & Béna, G. 2010. Partner choice in Medicago Truncatula–Sinorhizobium symbiosis. *Proceedings of the Royal Society B: Biological Sciences*, 277, 1947-1951.

Gumert, M. 2007a. Grooming and infant handling interchange in *Macaca fascicularis*: the relationship between infant supply and grooming payment. *International Journal of Primatology*, 28, 1059-1074.

Gumert, M. D. 2007b. Payment for sex in a macaque mating market. *Animal Behaviour*, 74, 1655-1667.

Gumert, M.D. & Ho, M-H.R. 2008. The trade balance of grooming and its coordination of reciprocation and tolerance in Indonesian long-tailed macaques (Macaca fascicularis). *Primates*, 49, 176-185.

Gust, D.A. 1994. A brief report on the social behavior of the crested mangabey (*Cercocebus galeritus galeritus*) with a comparison to the sooty mangabeys (*C. torquatus atys*). *Primates*, 35, 375-383.

Gust, D.A., Gordon, T.P. & Gergits, W. 1995. Proximity at birth relates to a sire's tolerance of his offspring among sooty mangabeys. *Animal Behaviour*, 49, 1403-1405.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I & II. *Journal of Theoretical Biology*, 7, 1-52.

Hamilton, W.D. 1971. Geometry of the selfish herd. *Journal of Theoretical Biology*, 31, 295-311.

Hammerstein, P. 1981. The role of asymmetries in animal contests. *Animal Behaviour*, 29, 193-205.

Hammerstein, P. 2003. Why is reciprocity so rare in social animals? A protestant appeal. In: *Genetic and cultural evolution of cooperation*. (ed. by P. Hammerstein), pp 83-93, the MIT Press, Cambridge, Massachussetts.

Hardin, G. 1968. The tragedy of the Commons. *Science*, 162, 1243-1248.

Hauser, M.D. 1988. Variation in maternal responsiveness in free-ranging vervet monkeys. A response to infant mortality risk? *American Naturalist*, 131, 573-587.

Heath, K. D. & Tiffin, P. 2009. Stabilizing mechanisms in a legume-rhizobium mutualism. *Evolution*, 63, 652-662.

Hemelrijk, C.K. 1994. Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*, 48, 479-481.

Hemelrijk, C. K. & Ek, A. 1991. Reciprocity and interchange of grooming and 'support' in captive chimpanzees. *Animal Behaviour*, 41, 923-935.

Hemelrijk, C.K. & Luteijn, M. 1998. Philopatry, male presence and grooming reciprocation among female primates: a comparative perspective. *Behavioural Ecology and Sociobiology*, 42, 207-215.

Hemelrijk, C.K., van Laere, G.J. & van Hooff, J.A.R.A.M. 1992. Sexual exchange relationships in captive chimpanzees? *Behavioral Ecology and Sociobiology*, 30, 269-275.

Henzi, S.P. & Barrett, L. 1999. The value of grooming to female primates. *Primates*, 40, 47-59.

Henzi, S.P. & Barrett, L. 2002. Infants as a commodity in a baboon market. *Animal Behaviour*, 63, 1-7.

Henzi, S. P., Barrett, L., Gaynor, D., Greeff, J., Weingrill, T. & Hill, R. A. 2003. Effect of resource competition on the long-term allocation of grooming by female baboons: evaluating Seyfarth's model. *Animal Behaviour*, 66, 931-938.

Holland, J. N. 2002. Benefits and costs of mutualism: demographic consequences in a pollinating seed-consumer interaction. *Proceedings of the Royal Society B-Biological Sciences*, 269, 1405-1412.

Holveck, M.-J. & Riebel, K. 2010. Low-quality females prefer low-quality males when choosing a mate. *Proceedings of the Royal Society B: Biological Sciences*, 277, 153-160.

Hinde, R.A. 1976. Interactions, relationships and social structure. *Man* 11, 1-17.

Hrdy, S.B. 1974. Male-male competition and infanticide among langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatologica*, 22, 19-58.

Hrdy, S.B. 1976. Care and exploitation of nonhuman primate infants by conspecifics other than the mother. In: *Advances in the Study of Behaviour. Vol. 6* (Ed. By J.S. Rosenblatt, R.A. Hinde, E. Shaw & C. Bier), pp. 101-158. New York: Academic Press.

Hrdy, S.B. 1977. *The langurs of Abu. Female and male strategies of reproduction*, Harvard University Press, Cambridge, MA.

Hrdy, S.B. 1978. Allomaternal care and abuse of infants among hanuman langurs. In: Recent Advances in Primatology. Vol. 1. (Ed. By D.J. Chivers & W.J. Herbert), pp. 169-172. London: Academic Press.

Hrdy, S.B. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, 1, 13-40.

Hrdy, S.B. & Hausfater, G. 1984. Comparative and evolutionnary perspectives on infanticide: introduction and overview. In: *Infanticide: Comparative and Evolutionary Perspectives*. G. (ed. by Hausfater and S.B. Hrdy). pp: xiii-xxxv, New York: Aldine de Gruyter.

Hrdy, S.B. & Whitten, P.L. 1987. Patterning of sexual activity. In: *Primate societies*. (ed by B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker). pp: 370-384, Chicago: Chicago University Press.

Hutchins, M. & Barash, D.P. 1976. Grooming in primates: implications for its utilitarian function. *Primates*, 17, 145-150.

Itani, J. & Nishimura, A. 1973. The study of infra-human culture in Japan. In: *Precultural primate behavior*. (ed. by Mensel E.), Basel: Karger, pp. 127-141.

Itoh, K. 2002. Personality research with non-human primates: theoretical formulation and methods. *Primates*, 43, 249-261.

Janson, C.H. 2000. Primate socio-ecology: the end of a golden age. *Evolutionary Anthropology*, 9, 73-86.

Janson, C.H. & van Schaik, C.P. 2000. The behavioral ecology of infanticide by males. In: *Infanticide by males and its implications*. (ed. by C.P. van Schaik and C.H. Janson). pp: 469-494, Cambridge: Cambridge University Press.

Johnstone, R.A. & Bshary, R. 2008. Mutualism, market effects and partner control. *Journal of Evolutionary Biology,* 21, 879-888.

Kawai, M. 1965. Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates*, 6, 1-30.

Keller, L. & Reeve, H.K. 1998. Familiarity breeds cooperation. *Nature*, 394, 121-122.

Keverne, E.B., Martensz, N. & Tuite, B. 1989. Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology*, 14, 155-161.

Kiers, E.T, Rousseau, R.A., West, S.A. & Denison, R.F. 2003. Host sanctions and the legume-rhizobium mutualism. *Nature*, 425, 78-81.

King, A.J. & Cowlishaw, G. 2009. Leaders, followers and group decision-making. *Communicative & Integrative Biol*ogy 2, 1-4.

Kohler, W. 1925. *The mentality of apes*. New York: Harcourt.

König, B. 1989. Kin recognition and maternal care under restricted feeding in house mice (*Mus domesticus*). *Ethology*, 82, 328-343.

Kosfeld, M., Heinrichs, M., Zak, P.J., Fischbacher, U. & Fehr, E. 2005. Oxytocin increases trust in humans. *Nature,* 435, 673-676.

Koyama, N. F., Caws, C. & Aureli, F. 2006. Interchange of grooming and agonistic support in chimpanzees. *International Journal of Primatology*, V27, 1293-1309.

Kralik, J.D., Hauser, M.D. & Zimlicki, R. 2002. The relationship between problem solving and inhibitory control: cotton-top tamarin (*Saguinus oedipus*) performance on a reversed contingency task. *Journal of Comparative Psychology*, 116, 39-50.

Krause, J. & Ruxton, G.D. 2002. *Living in groups*. (ed by Harvey, P.H. and R.M. May) Oxford University press.

Kummel, M. & Salant, S. W. 2006. The economics of mutualisms: optimal utilization of mycorrhizal mutualistic partners by plants. *Ecology*, 87, 892-902.

Kutsukake, N. & Clutton-Brock, T. H. 2008. The number of subordinates moderates intrasexual competition among males in cooperatively breeding meerkats. *Proceedings of the Royal Society B: Biological Sciences*, 275, 209-216.

Kutsukake, N. & Clutton-Brock, T. H. 2010. Grooming and the value of social relationships in cooperatively breeding meerkats. *Animal Behaviour*, 79, 271-279.

Lancaster, J. B. 1971. Play-mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys (Cercopithecus aethiops). *Folia primatologica*, 15, 161-182.

Lazaro-Perea, C., de Fátima Arruda, M. & Snowdon, C.T. 2004. Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. *Animal Behaviour*, 67, 627-636.

Lehmann, L. & Keller, L. 2006. The evolution of cooperation and altruism. A general framework and classification of models. *Journal of Evolutionary Biology*, 19, 1365-1725.

Lehmann, J., Korstjens, A.H. & Dunbar, R.I.M. 2007. Group size, grooming and social cohesion in primates. *Animal Behaviour,* 74, 1617-1629.

Leimar, O. & Axén, A. 1993. Strategic behaviour in an interspecific mutualism: interactions between lycaenid larvae and ants. *Anima Behaviour*, 46, 1177-1182.

Lewis, R.J. 2002. Beyond dominance: the importance of leverage. *Quarterly Review of Biology*, 77, 149-164.

Löttker, P., Huck, M., Zinner, D. P. & Heymann, E. W. 2007. Grooming relationships between breeding females and adult group members in cooperatively breeding moustached tamarins *(Saguinus mystax)*. *American Journal of Primatology*, 69, 1-14.

Macfarlan, S. J. 2010. The logic of labor exchange in a Dominican village: competitive altruism, biologic markets, and the nexus of male social relations. Washington State University.

Maestripieri, D. 1994. Social structure, infant handling, and mother styles in group-living Old World monkeys. *International Journal of Primatology*, 15, 531-553.

Mangel, M. 1990. Resource divisibility, predation and group formation. *Animal Behaviour,* 39, 1163-1172.

Manson, J. H. 1999. Infant handling in wild Cebus capucinus: Testing bonds between females? *Animal Behaviour*, 57, 911–921.

Manson, J.H, Navarrete, C.D., Silk, J.B & Perry, S. 2004. Time-matched grooming in female primates? New analyses from two species. *Animal Behaviour*, 67, 493-500.

Matsumura, S. 1997. Mothers in a wild group of moor macaques (*Macaca maura*) are more attractive to others when holding their infants. *Folia Primatologica*, 68, 77-85.

Melis, A. P., Hare, B. & Tomasello, M. 2008. Do chimpanzees reciprocate received favours? *Animal Behaviour*, 76, 951-962.

Metz, M., Klump, G. & Friedl, T. 2007. Temporal changes in demand for and supply of nests in red bishops (Euplectes orix): dynamics of a biological market. *Behavioral Ecology and Sociobiology*, 61, 1369-1381.

Milinski, M. 1987. Tit for Tat in sticklebacks and the evolution of cooperation. *Nature*, 325, 433-435

Mineka, S. & Cook, M. 1988. Social learning and the acquisition of snake fear in monkeys. In: *Social learning psychological and biological perspectives*. (ed. by Zentall, T.R. & Galef, B.G.). Hillsdale, NJ: Lawrence Erlbaum Inc. pp. 51-74.

Mohnot, S.M. 1971. Some aspects of social changes and infant killing in the Hanuman langur (*Presbytis entellus*) (Primates: *Cercopithecidae*) in Western India. *Mammalia*, 35, 175-198.

Morhenn, V.B., Park, J.W., Piper, E. & Zak, P.J. 2008. Monetary sacrifice among strangers is mediated by endogenous oxytocin release after physical contact. *Evolutionary Human Behaviour,* 29, 375-383.

Mooring, M.S., McKenzie, A.A. & Hart, B.L. 1996. Role of sex and breeding status in grooming and total load of impala. *Behavioural Ecology and Sociobiology*, 39, 259-266.

Muroyama, Y. 1994. Exchange of grooming for allomothering in female patas monkeys. *Behaviour* 128, 103-129.

Narum, S.R. 2006. Beyond Bonferroni: Less conservative analyses for conservation genetics. *Conservation Genetics*, 7, 783-787.

Niemeyer, C.L. & Anderson, J.R. 1983. Primate harassment of matings. *Ethology and Sociobiology*, 4, 205-220.

Noë, R. 1990. A veto game played by baboons: a challenge to the use of the Prisoner's Dilemma as a paradigm for reciprocity and cooperation. *Animal Behaviour*, 39, 78-90.

Noë, R. 2001. Biological markets: partner choice as the driving force behind the evolution of mutualisms. In *Economics in nature. Social dilemmas, mate choice and biological markets*. (ed by R. Noë, J.A.R.A.M. van Hoof and P. Hammerstein), pp 93-118, Cambridge University Press.

Noë, R. 2005. Digging for the roots of trading. In: *Cooperation in Primates and Humans. Mechanisms and Evolution*. (ed. by P.M. Kappeler & C.P. van Schaik), Springer, Heidelberg, pp 233-261.

Noë, R & Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioural Ecology and Sociobiology*, 35, 1-11.

Noë, R & Hammerstein, P. 1995. Biological markets. *Trends in Ecology and Evolution*, 10, 336-339.

Noë, R. & Sluijter, A.A. 1990. Which adult male savanna baboons form coalitions? *International Journal of Primatology*, 16, 77-165.

Noë, R. & Sluijter, A. A. 1995. Which adult male savanna baboons form coalitions? *International Journal of Primatology*, 16, 77-105.

Noë, R., Schaik, C. P. & Hooff, J. A. R. A. M. 1991. The market effect: an explanation for pay-off asymmetries among collaborating animals. *Ethology*, 87, 97-118.

Norscia, I., Antonacci, D. & Palagi, E. 2009. Mating first, mating more: biological market fluctuation in a wild prosimian. *PLoS ONE*, 4, 46-79.

Norton, G.W. 1986. Leadership: decision processes of group movement in yellow baboons. In Primate ecology and conservation. (ed by J.G.L. Else), Cambridge University Press, Cambridge).

Nunn, C.L. 1999. The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour*, 58, 229-246.

Ottoni, E.B., Dogo de Resende, B. & Izar P. 2005. Watching the best nutcrackers: what capuchin monkeys (Cebus apella) know about others' tool using skills. *Animal Cognition*, 24, 215-219.

Packer, C. 1977. Reciprocal altruism in Papio anubis. *Nature*, 265, 441-444.

Palombit, R.A. 1999. Infanticide and the evolution of pair bonds in nonhuman primates. *Evolutionary Anthropology*, 7, 117-129.

Palombit, R.A. 2000. Infanticide and the evolution of male-female bonds in animals. In *Infanticide by males and its implications*. (Ed. by C.P. van Schaik & C.H. Janson). pp: 239-268. Cambridge: Cambridge University Press.

Palombit, R.A., Seyfarth, R.M. & Cheney, D.L. 1997. The adaptive value of 'friendships' to female baboons: experimental and observational evidence. *Animal Behaviour*, 54, 599-614.

Palombit, R.A., Cheney, D.L. & Seyfarth, R.M. 2001. Female-female competition for male 'friends' in wild chacma baboons, *Papio cynocephalus ursinus*. *Animal behaviour*, 61, 1159-1171.

Pawlowski, B. & Dunbar, R. I. M. 1999. Impact of market value on human mate choice decisions. *Proceedings of the Royal Society, London, B.*, 266, 281-285.

Payne, H.F.P., Lawes, M.J. & Henzi, S.P. 2003. Competition and the exchange of grooming in female samango monkeys (Cercopithecus mitis erytharcus). *Behaviour*, 140: 453-471.

Pearce, J.M. 2008. *Animal learning and cognition. An introduction*. 3rd ed. Psychology Press.

Pellmyr, O. 1997. Pollinating seed eaters: why is active pollination so rare? *Ecology*, 78, 1655-1660.

Pellmyr, O. & Huth, C.J. 1994. Evolutionary stability of mutualism between yuccas and yucca moths. *Nature*, 372, 257-260.

Pellmyr, O. & Leebens-Mack, J. 1999. Forty million years of mutualism: evidence for Eocene origin of the yucca-yucca moth association. *Proceedings of the National Academy of Sciences*, 96, 9178-9183.

Pellmyr, O., Leebens-Mack, J. & Huth, C.J. 1996. Non-mutualistic yucca moths and their evolutionary consequences. *Nature*, 380, 155-156.

Perry, S. 2009. Conformism in the food processing techniques of white-faced capuchin monkeys (*Cebus capucinus*). *Animal Cognition*, 12, 705–716.

Petit, O. & Thierry, B. 1992. Affiliative function of the silent bared-teeth display in moor macaques (Macaca maurus): further evidence for the particular status of Sulawesi macaques. *International Journal of Primatology*, 13, 97-105.

Perez, A. & Vea, J. J. 2000. Functional implications of allogrooming in Cercocebus torquatus. *International Journal of Primatology*, 21, 255-267.

Perez, A. P. & Baro, J. J. V. 1999. Does allogrooming serve a hygienic function in Cercocebus torquatus lunulatus? *American Journal of Primatology*, 49, 223-242.

Pierce, N.E., Braby, M.F., Heath, A., Lohman, D.J., Mathew, J., Rand, D.B. & Travassos, M.A. 2002. The ecology and evolution of ant association in the lycaenidae (Lepidoptera). *Annual Review of Entomology*, 47, 733-771.

Pollet, T. V. & Nettle, D. 2008. Driving a hard bargain: sex ratio and male marriage success in a historical US population. *Biology Letters*, 4, 31-33.

Pollet, T. V. & Nettle, D. 2009. Market forces affect patterns of polygyny in Uganda. *Proceedings of the National Academy of Sciences*, 106, 2114-2117.

Port, M., Clough, D. & Kappeler, P.M. 2008. Market effects offset the reciprocation of grooming in free-ranging redfronted lemurs, *Eulemur fulvus rufus*. *Animal Behaviour*, 77, 29-36.

Premack, D. 1976. *Intelligence in ape and man*. Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.

Price, E.E., Lambeth, S.P., Schapiro, S.J. & Whiten, A. 2009. A potent effect of observational learning on chimpanzee tool construction. *Proceedings of Royal Society B*., 276, 3377-3383.

Pruetz, J.D. & Isbell, L.A. 2000. Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. *Behavioural Ecology and Sociobiology*, 49, 38-47.

Pusey, A.E. & Packer, C. 1994. Infanticide in lions: consequences and counterstrategies. In: *Infanticide and Parental Care*. (ed. by S. Parmigiani and F.S. vom Saal). pp: 277-300, F.S. Chur (Switzerland): Harwood Academic Publishers.

Radford, A. N. & Du Plessis, M. A. 2006. Dual function of allopreening in the cooperatively breeding green woodhoopoe, Phoeniculus purpureus. *Behavioral Ecology and Sociobiology*, 61, 221-230.

Ramseyer, A., Pelé, M., Dufour, V., Chauvin, C. & Thierry, B. 2006. Accepting loss: the temporal limits of reciprocity in brown capuchin monkeys. *Proceedings of the Royal Society B.*, 273, 179-184.

Range, F. & Noë, R. 2002. Familiarity and dominance relations among female sooty mangabeys in the Taï National Park. *American Journal of Primatology*, 56, 137-153.

Rankin, D.J., Bargum, K. & Kokko, H. 2007. The tragedy of the commons in evolutionary biology. *TREE,* 22: 643-651.

Ranta, E., Peuhkuri, N., Laurila, A., Rita, H. & Metcalfe, N.B. 1996. Producers, scroungers and foraging group structure. *Animal Behaviour*, 51, 171-175.

Reyer, H.U. 1986. Breeder-helper-interactions in the pied kingfisher reflect the costs and benefits of cooperative breeding. *Behaviour*, 96, 277-303.

Ridley, M. 2004. *Evolution*. 3rd ed. Oxford Blackwell Scientific.

Roberts, G. & Sherratt, T. 1998. Development of co-operative relationships through increasing investment. *Nature*, 394, 175-179.

Rowell, T.E. 1972. Female reproductive cycles and social behavior in primates. *Advances in Study of Behaviour,* 4, 69-105.

Rowell, T.E. & Chalmers, N.R. 1970. Reproductive cycles of the mangabey, *Cercocebus albigena. Folia primatologica*, 12, 264-272.

Rubenstein, D. I. 1986. Ecology and sociality in horses and zebras. In *Ecological Aspects of Social Evolution*. (Ed by D.I. Rubenstein & R.W. Wrangham)

de Ruiter, J.R. & van Hooff, J.A.R.A.M. 1993. Male dominance rank and reproductive success in primate groups. *Primates*, 34, 513-523.

Russon, A.E. & Galdikas, B.M.F. 1993. Imitation in free-ranging orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, 107, 147-161.

Ryan, M.J. 1997. Sexual selection and mate choice. In *Behavioural Ecology*, 4th ed., (Ed. by J.R. Krebs & N.B. Davies), pp: 179-202. Cambridge: Cambridge University Press.

Sabbatini, G. & Visalberghi, E. 2008. Inferences about the location in capuchin monkeys (*Cebus apella*) in two sensory modalities. *Journal of Comparative Psychology*, 122, 156-166.

Sachs, J.L., Mueller, U.G., Wilcox, T.P. & Bull, J.J. 2004. The evolution of cooperation. *The Quarterly Review of Biology*, 79, 135-160.

Sapolsky, R. M. 2005. The influence of social hierarchy on primate health. *Science*, 308, 648-652.

Schaffner, C.M. & Aureli, F. 2005. Embraces and grooming in captive spider monkeys. *International Journal of Primatology*, 26, 1093-1106.

van Schaik, C.P. 2000. Vulnerability to infanticide by males: patterns among mammals. In: *Infanticide by males and its implications*. (ed. by C.P. van Schaik and C.H. Janson). pp: 61-71, Cambridge: Cambridge University Press.

van Schaik, C.P. and Kappeler, P.M. 1997. Infanticide risk and the evolution of male-female association in primates. *Proceedings of Royal Society B*., 264, 1687-1694.

van Schaik, C.P., van Noordwijk, M.A. & Nunn, C.L. 1999. Sex and social evolution in primates. In: *Comparative Primate Socioecology*. (ed. by P.C. Lee). pp: 204-240, Cambridge: Cambridge University Press.

Scharlemann, J.P.W, Eckel, C.C., Kacelnik, A. & Wilson, R.K. 2001. The value of a smile: game theory with a human face. *Journal of Economic Psychology*, 22, 617-640.

Schino, G. 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, 18, 115-120.

Schino, G. & Pellegrini, B. 2009. Grooming in mandrills and the time frame of reciprocal partner choice. *American Journal of Primatology*, 71, 883-888.

Schino, G., Polizzi di Sorrentino, E. & Tiddi, B. 2007. Grooming and coalitions in Japanese macaques *(Macaca fuscata)*: partner choice and the time frame of reciprocation. *Journal of Comparative Psychology*, 121, 181-188.

Schino, G., Ventura, R. & Troisi, A. 2003. Grooming among female Japanese macaques : distinguishing between reciprocation and interchange. *Behavioral Ecology*, 14, 887-891.

Schmidt, K.L & Cohn, J.F. 2001. Human facial expressions as adaptations: evolutionary questions in facial expression research. *Yearbook of Physical Anthropology*, 44, 3-24.

Schwartz, M.W. & Hoeksema, J.D. 1998. Specialization and resource trade: biological markets as a model of mutualisms. *Ecology*, 79, 1029-1038.

Segraves, K. A., Althoff, D. M. & Pellmyr, O. 2005. Limiting cheaters in mutualism: evidence from hybridization between mutualist and cheater yucca moths. *Proceedings of the Royal Society, London, B.*, 272, 2195 - 2201.

Seyfarth, R. M. 1977. A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, 65, 671–698.

Seyfarth, R.M. & Cheney, D.L. 1984. Grooming, alliances, and reciprocal altruism in vervet monkeys. *Nature*, 308, 541-543.

Shumaker, R.W., Palkovich, A.M., Beck, B.B., Guagnano, G.A. & Morowitz, H. 2001. Spontaneous use of magnitude discrimination and ordination by the orangutan (*Pongo pygmaeus*). *Journal of Comparative Psychology*, 115, 385-391.

Siegel, S. & Castellan, N.J. 1988. *Non Parametric Statistics for the Behavioural Sciences*. Singapore: McGraw-Hill Book company.

Silk, J.B. 1980. Kidnapping and female competition in captive bonnet macaques. *Primates*, 21, 100-110.

Silk, J.B. 1999. Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour*, 57, 1021-1032.

Silk, J.B. 2003. Cooperation without counting. The puzzle of friendship. In: *Genetic and cultural evolution of cooperation*. (ed. by P. Hammerstein), pp 83-93, the MIT Press, Cambridge, Massachussetts.

Silk, J.B. 2007. Social components of fitness in primate groups. *Science*, 317, 1347-1351.

Silk, J. B., Alberts, S. C. & Altmann, J. 2004. Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Animal Behaviour*, 67, 573-582.

Simms, E. L. T., Povich, D. L. J., Shefferson, R. P., Sachs, J. L., Urbina, M. & Tausczik, Y. 2006. An empirical test of partner choice mechanisms in a wild legume-rhizobium interaction. *Proceedings of the Royal Society B.*, 273, 77-81.

Slater, K.Y., Schaffner, C.M. & Aureli, F. 2007. Embraces for infant handling in spider monkeys: evidence for a biological market? *Animal Behaviour*, 74, 455-461.

Smith, J. E., Memenis, S. K. & Holekamp, K. E. 2007. Rank-related partner choice in the fission–fusion society of the spotted hyena (Crocuta crocuta). *Behavioral Ecology and Sociobiology*, 61, 753-765.

Smuts, B.B. & Smuts, R.W. 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behaviour*, 22, 1-61.

Soares, M. C., Bshary, R., Cardoso, S. C. & Cote, I. M. 2008. Does competition for clients increase service quality in cleaning gobies? *Ethology*, 114, 625-632.

Sokal, R.R. & Rohlf, F.J. 1995. *Biometry*. 3rd ed. W.H. Freeman and Company. Basingstoke, England.

Soltis, J., Thomsen, R., Matsubayashi, K. & Takenaka, 0. 2000. Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). *Behavioural Ecology and Sociobiology*, 48, 195-202.

Sommer, V. 1994. Infanticide among the langurs of Jodhpur: testing the sexual selection hypothesis with a long-term record. In: *Infanticide and Parental Care*. (ed. by S. Parmigiani and F.S. vom Saal). pp: 155-198, F.S. Chur (Switzerland): Harwood Academic Publishers.

Stammbach, E. 1988. Group responses to specially skilled individuals in a *Macaca fascicularis* group. *Behaviour*, 107, 241-266.

Stephens, D.W., McLinn, C.M. & Stevens, J.R. 2002. Discounting and reciprocity in an iterated Prisoner's Dilemma. *Science*, 298, 2216-2218.

Stevens, J.R., Cushman, F.A. & Hauser, M.D. 2005 a. Evolving the psychological mechanisms

for cooperation. *Annual Review of Ecology, Evolution, and Systematics*, 36, 499-518.

Stevens, J.R., Hallinan, E.V. & Hauser, M.D. 2005 b. The ecology and evolution of patience in two new world monkeys. *Biology Letters*, 1, 223-226.

Stevens, J. R. & Stephens, D. W. 2008. Patience. *Current Biology*, 18, R11-R12

Stopka, P & Macdonald, D.W. 1999. The market effect in the wood mouse, *Apodemus sylvaticus*: selling information on reproductive status. *Ethology*, 105, 969-982.

Sussman, R.W., Cheverud, J.M. & Bartlett, T.Q. 1995. Infant killing as an evolutionary strategy: reality or myth? *Evolutionary Anthropology*, 3, 149-151.

Templeton, J.J. & Giraldeau, L.A. 1995. Public information cues affect the scrounging decisions of starlings. *Animal Behaviour*, 49, 1617-1626.

Thierry, B. & Anderson, J.R. 1986. Adoption in anthropoid primates. *International Journal of Primatology*, 7, 191-216.

Thorndike, E.L. 1911. *Animal intelligence: experimental studies*. New York: Macmillan.

Thorpe, W.H. 2008. The learning abilities of birds. *Ibis*, 93, 252-296.

Tiddi, B., Aureli, F. & Schino, G. 2010. Grooming for infant handling in tufted capuchin monkeys: a reappraisal of the primate infant market. *Animal Behaviour*, 79, 1115-1123.

Tobin, H., Logue, A.W., Chelonis, J.J., Ackerman, K.T. & May III, J.G. 1996. Self-control in the monkey *Macaca fascicularis*. *Animal Learning & Behavior*, 24, 168-174.

Treves, A. 1998. Primate social system: conspecific threat and coercion-defence hypotheses. *Folia Primatologica*, 69, 81-88.

Treves, A. 2000. Prevention of infanticide: the perspective of infant primates. In: *Infanticide by males and its implications*. (ed. by C.P. van Schaik and C.H. Janson). pp: 223-238, Cambridge: Cambridge University Press.

Trivers, R.L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology*, 46, 35-57.

Trivers, R. 1972. Parental investment and sexual selection. In *Sexual selection and the Descent of man 1871-1971*. (Ed. by B. Campbell), pp: 136-179. Chicago: Aldine.

Trivers, R. 1985. Parental investment and sexual selection. In *Social evolution*. (Ed by J.W. Behnke & J. Andrews), pp: 203-238. The Benjamin/Cummings Publishing Company.

Ventura, R., Majolo, B., Koyama, N. F., Hardie, S. & Schino, G. 2006. Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. *American Journal of Primatology*, 68, 1138-1149.

Visalberghi, E. & Trinca, L. 1989. Tool use in capuchin monkeys: distinguishing between performance and understanding. *Primates*, 30: 511–521.

de Vries, H., Netto, W. J. & Hanegraaf, P. L. H. 1993. MATMAN: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour 125:157-175*.

de Waal, F. B. M. 1997. The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior*, 18, 375-386.

de Waal, F. B. M. 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour,* 60, 253-261.

de Waal, F. B. M. & Yoshihara, D. 1983. Reconciliation and redirected affection in rhesus monkeys. *Behaviour,* 85, 224-241.

Ward, P. & Zahavi, A. 1973. The importance of certain assemblages of birds as 'information centres' for food finding. *Ibis*, 115, 517-534.

Watts, D. P. 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, 139, 343-370.

Weingrill, T. 2000. Infanticide and the value of male-female relationships in mountain chacma baboons. *Behaviour*, 137, 337-359.

West, S.A., Griffin, A.S. & Gardner, A. 2007a. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, 20, 415-432.

West, S.A., Griffin, A.S. & Gardner, A. 2007b. Evolutionary explanations for cooperation. *Current Biology*, 17, 61-672.

West, S.A., Kiers, E.T., Simms, E.L. & Denison, R.F. 2002. Sanctions and mutualism stability: why do rhizobia fix nitrogen? *Proceedings of the Royal Society B.*, 269, 685-694.

Whitmore, T.C. 1990. *An introduction to tropical rain forests*. Oxford: Oxford Clarendon Press.

Whitten, P.L. & Russell, E. 1996. Information content of sexual swellings and fecal steroids in sooty mangabeys (*Cercocebus torquatus atys*). *American Journal of Primatology*, 40, 67-82.

Wilkinson, G. S. 1984. Reciprocal food sharing in vampire bats, *Nature,* 309, 181-184.

Witting, R.M. & Boesch, C. 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Taï National Park. *International Journal of Primatology*, 24, 847-867.

Wolff, J.O. & Macdonald, D.W. 2004. Promiscuous females protect their offspring. *Trends in Ecology and Evolution*, 19, 127-134.

Wrangham, R.W. 1987. Evolution of social structure. In *Primate Societies*. (Ed by B.B. Smuts, D.L. Cheney, R.W. Seyfarth, R.W. Wrangham & T.T. Struhsaker), pp: 121-134. Chicago: Chicago University Press.

Wrangham, R. W. & Rubenstein, D. I. 1986. Social evolution in birds and mammals. In *Ecological Aspects of Social Evolution*. (Ed by D.I. Rubenstein & R.W. Wrangham).

Wright, P.C. 1995. Demography and life history of free ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *International Journal of Primatology*, 16, 835-854.

Zahavi, A. 1975. Mate selection – a selection for a handicap. *Journal of Theoretical Biology*, 53, 205-214.

Zahavi, A. & Zahavi, A. 1997. *The handicap principle*. New York: Oxford University Press.

Zamma, K. 2002. Grooming site preferences determined by lice infection among Japanese macaques in Arashiyama. *Primates*, 43, 41-49.

Zinner, D. & Deschner, T. 2000. Sexual swellings in female hamadryas baboons after male take-overs: "deceptive" swellings as a possible female counter-strategy against infanticide. *American Journal of Primatology*, 52, 157-168.